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Biogeography and Timing of Evolutionary Events among Great Basin Fishes

*G.R. Smith, T.E. Dowling, K.W. Gobalet, T. Lugaski,
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ABSTRACT

Hubbs and Miller's Great Basin works are model studies of the evolution of isolated endemic aquatic organisms and of hydrographic history. They investigated spatial and temporal barriers that permitted evolutionary divergence of fishes. They also used fish evidence to identify the locations and possible timings of past aquatic connections among basins. Hubbs and Miller focused on morphological differences among fish populations in related basins and hypothesized that their evolutionary divergence occurred over only hundreds to thousands of years. Their conclusions depended upon the assumption that divergence began after the most recent time of homogeneous ancestral populations, which was assumed to be the time of closure of the most recent hydrographic connection. This approach and its key assumptions are standard in studies of evolutionary rates, but they require reexamination.

Our data suggest that rates of morphological change in oligogenic and ecophenotypic traits of Great Basin fishes may be rapid in the short term (thousands of years), but Miocene to Pleistocene fossils of western North American fishes indicate slow changes over millions of years. Tests of hypotheses about evolutionary rates require independent estimates of both time and degree of divergence. Our evolutionary-rate estimates are based upon regression of percent sequence divergence (of mitochondrial DNA) between pairs of lineages against millions of years of diver-

gence of sister clades, estimated from dates of first appearances in the fossil record. The results indicate rates of molecular evolution in the range of approximately one-half percent (salmonids) to one percent (cyprinids and cyprinodonts) sequence divergence per one million years. The ages of some forms thought to represent ten thousand years of postpluvial evolution are more likely to be hundreds of thousands of years old, according to molecular/fossil estimates. Estimated divergence times of fishes, based upon DNA, provide unique data on the nature and timing of barriers and aquatic connections among basins.

Great Basin fish faunas exhibit high endemism, but they have lower diversity than predicted by pluvial cycles of isolation and by rapid evolution in allopatry. We hypothesize that uplift causes high stream gradients and, therefore, decreased local habitat diversity because of rapid stream runoff. Small and isolated populations on the basin floors are prone to allopatric differentiation, but they also are prone to high extinction rates; therefore, isolation and stabilizing selection in desert basins rarely produced new species that survived extinction events.

Dedication

This paper is dedicated to Carl L. Hubbs, Robert R. Miller, and Dwight W. Taylor, whose studies of aquatic organisms in western North American desert basins set the twentieth century standard for aquatic biogeography and conservation.

Introduction to Great Basin Ichthyology

Carl L. Hubbs began his studies of fishes in the Great Basin in 1915 while on an expedition to the Bonneville Basin as a field assistant to J.O. Snyder (Miller and Shor, 1997). Prior to the Bonneville trip, Snyder had surveyed fishes in the Lahontan Basin and in the Oregon Lakes, Owens River, and Mohave River basins (Snyder, 1908, 1912, 1914, 1917a, 1917b, 1918, 1919, 1924). Hubbs continued to conduct exhaustive explorations of the Great Basin in 1934, 1938, and 1942; with his wife, Laura, and their children, Earl, Frances, and Clark, he collected and identified more than 118,000 specimens. Hubbs was joined by his student, Robert Miller, in 1938, and between them they

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produced about three dozen papers on Great Basin fishes. Miller's efforts resulted in numerous papers on fishes of the Death Valley system (e.g., 1946a, 1946b, 1950, 1972) and on broader issues relating to evolution and conservation of Great Basin fishes (1959, 1961a, 1961b, 1965, 1981). Miller continued conducting this field work with his wife, Frances Hubbs Miller, and their five children, and he extended the project to include a survey of the fishes of Mexico.

The landmark synthesis of the systematics and biogeography of fishes of the Great Basin was published by Carl Hubbs and Robert Miller in 1948(b), which was expanded from a symposium paper read in 1942. The monograph described the geographical limits of more than 100 hydrographic units, the elevations of ancient lake levels, and the biogeographic relationships of fishes in each basin. The authors' goal was to show how convincingly physiographic deductions are supported by knowledge of the distribution of fishes in the Great Basin.

The Hubbs–Miller team and Elliot Blackwelder (1933) both used fish distributions to infer past aquatic connections, which were based upon the principles of Jordan (1905, chapters 16, 17). The interaction of time and barriers framed the questions in the Hubbs–Miller inventory of Great Basin fish evolution. Their descriptions and classification of those fishes were intended to answer questions about hydrographic connections among basins, barriers between basins, and rapidity of evolution. Although they chose not to speculate about evolutionary mechanisms (1908b:119), they offered frequent hypotheses about amounts and rates of evolution. They later expanded upon their ideas about fish speciation (Hubbs, 1940, 1941a, 1941b; Miller, 1946a, 1950).

Hubbs and Miller's most exciting idea was declared in the introduction to their 1948 monograph (Hubbs and Miller, 1948b:24):

Some of the isolation and speciation that is dated from Pleistocene time may be much more recent. Now disconnected waters within many of the basins of western North America may have been connected and their fish fauna made uniform not many centuries ago. From a consideration of the evidences on climatic changes ... it seems likely that such connections may have been established several times during the last three millennia. We believe, however, that most of the local differentiation and endemism among the fishes of the isolated desert waters dates from the end of the Glacial period. Hutchinson (1939) concluded that the similar differentiation of now isolated fish populations in Kashmir and Indian Tibet dates from the period of maximum glaciation. ...

In correlation with Post-pluvial isolation, a limited degree of speciation has occurred here and there, but data are too meager to warrant any attempt to use the rate of species evolution in dating the Pluvial waters. ... A considerable body of observations and mathematical data indicates that small, closely inbreeding populations may speciate at a much more rapid rate than was previously thought possible (Wright, 1940a, 1940b, 1942; Huxley, 1943).

The authors treated their geological and ichthyological data in two ways: they used geological data to infer rates of fish differentiation, and they used degree of morphological divergence to infer the times of geological barriers. The usual assumption was that fish populations were uniform at the end of the most recent connection between aquatic habitats. This led to the de-

duction that rapid speciation occurred in the postpluvial interval of isolation, about 11,000 years.

Carl Hubbs, Robert Miller, and Laura C. Hubbs (1974) expanded upon their previous work and the work of others in their subsequent monograph on hydrographic history and relict fishes of the North-Central Great Basin. Laura Hubbs measured hundreds of fish specimens from different basins and calculated the mean and standard deviation for the populations in each basin, providing replicated comparisons of times and amounts of divergence. Hubbs and Miller (1948a, 1972) described many additional localized cyprinid species and subspecies, which provided further evidence for postpluvial divergence in geographic isolation (see Appendix).

Hubbs and Miller sought to answer a question that still motivates biogeographers (e.g., Ricklefs and Schluter, 1993); that is, What are the appropriate scales of the spatial and temporal interactions that bring about species production? Hubbs and Miller (1948b) emphasized differences among and within basins, namely, different taxonomic levels, numbers of endemic forms, and local diversity in relation to regional diversity as indicators of evolutionary history: "The Lahontan fauna ... comprises, we estimate, about 30 forms, as compared with perhaps 28 in the Bonneville and about 24 in the Death Valley system. The relatively high number of total forms is correlated with the isolation of local populations, for the Lahontan system has become greatly disrupted since Pluvial times" (Hubbs and Miller, 1948b:32).

Hubbs and Miller (1948b:41) also recognized an important role for hybridization in evolution: "Since the waters have dwindled, and the lake and creek types have been forced into cohabitation, the two have hybridized very extensively. We have referred to this specific breakdown in connection with our analysis of a similar case of hybridization in the Mohave Desert (Hubbs and Miller, 1943)." The effects of hybridization in reducing diversity and erasing evidence of evolutionary history are peculiarly prominent among fishes in the western United States (Smith, 1992a; Dowling and Secor, 1997).

Our goal is to continue the comparison of fish and hydrographic information so as to answer questions about timing and origins of fish diversity. Evidence presented herein for timing of fish divergence comes from the fossil record (G.R. Smith, 1981a, 1981b; Smith et al., 1982) and from molecular studies (Dowling et al., 2002; Shiozawa and Evans, unpublished). In this paper, we summarize gene sequence divergence data in the context of the fossil record of Great Basin fishes. We seek to shed light on the rates of evolutionary changes in Great Basin drainages in the spirit of the other Great Basin naturalists of 50 years ago (Hall, 1946:59–67; Durrant, 1952:490–518; LaRivers, 1962; and the vast body of literature published by Hubbs and Miller).

Our understanding of freshwater fish distributions benefits from the fact that freshwater fish are more geographically constrained than most other organisms (Cope, 1868; Jordan, 1905). The principles thought to influence distribution and evolution

of fishes have remained rather constant during the last 130 years, but estimates of timing of geological and evolutionary events vary by five orders of magnitude (compare Cope, 1868, with Hubbs et al., 1974). The Great Basin offers a unique opportunity to study the time scales of evolutionary processes because of its numerous, isolated basins that have replicated fish habitats and histories. In addition, well-documented evidence exists for environmental gradients, pluvial cycles, and ages of sediments that preserve fossil ancestors of Holocene fishes (e.g., Morrison, 1965, 1991; Benson and Thompson, 1987; Benson et al., 1990; Oviatt et al., 1992; Reheis and Morrison, 1997; Smith and Bischoff, 1997). These factors provide the basis for Cope's (1883) and Hubbs and Miller's (1948b) assumption that fish evidence can contribute much to the study of hydrographic history. Our attempts to fulfill this promise have been guided further by Dwight Taylor's methods and his principle (1960) that hydrologic, topographic, and climatic features change more rapidly than do lineages of organisms.

The Late Cenozoic fossil record in the Great Basin reflects the climatic and faunal revolution between the Paleogene and the Neogene. For example, the temperate Miocene to Holocene fish faunas of the Great Basin (as now known) share only one family (Catostomidae) with the subtropical faunas of the western North American Eocene in Wyoming, Utah, and Colorado (Grande, 1984). Transitional Great Basin fish records are Cope's (1872) *Amyzon mentalis* and *Trichophanes hians* from the Osino, Nevada, Oligocene coal beds and Early Tertiary fossils similar to *Diplomystus* in Elko County, Nevada. Our discussion herein, however, will be limited to the late Cenozoic record. Publications on fossil *Empetrichthys*, fundulids, and cyprinodontids by Miller (1945b) and Uyeno and Miller (1962) included reviews of many pre-Pleistocene records of modern lineages in the southwestern Great Basin. LaRivers (1962) compiled the first account of endemic and introduced fishes in Nevada, including what was known at that time about ecology and fossil fishes.

Newberry (1871, and references therein) was the first to study Great Basin fishes from a geological context, but he was soon followed by Jordan (1878a, 1878b, 1891), Cope (1883), Jordan and Evermann (1896), and Tanner (1936). J.O. Snyder and Hubbs and Miller, in works cited above, were the next to dominate the field. Uyeno and Miller (1962), Miller (1981), M.L. Smith (1981), and G.R. Smith (1966, 1978, 1981a, 1981b) discussed fossils and described patterns of differentiation, species density, and zoogeography of western North American fishes among basins. Minckley et al. (1986) discussed this history in detail, then compiled current geological literature on the Cenozoic tectonics of western North America and hypothesized broad aspects of zoogeographic history of western fishes. They looked for congruence between area cladograms and fish cladograms then available and concluded that the modern fauna occupied western tectonic units in the Oligocene before they were separated from Atlantic Ocean tributaries by the Miocene cycle of tectonic uplift. Minckley and

Deacon (1991) described critical conservation issues and extinction threats to the modern fauna. Behnke (1992) provided original analysis and summarized the available information on recent trouts. Sigler and Sigler (1987, 1996) summarized the modern fauna, including introduced fishes.

The fishes discussed in the present paper inhabit or inhabited the hydrographic Great Basin, as defined, for example, by Hubbs and Miller (1948b) as being the region of Holocene internal drainage bounded by barriers shared with the present drainages of the Colorado, Sacramento, Klamath, and Columbia Rivers (Figure 1). The Great Basin is not static; rather, it is a mosaic whose boundaries and external connections have shifted with tectonic, volcanic, and climatic changes across time scales ranging from 10 thousand years (Ky) to 10 million years (My) during the last 17 My (Minckley et al., 1986; and citations below). Many hydrographic connections have been hypothesized. For example, in the middle Miocene, there were large lakes in northern Nevada and Utah that drained through the Snake River Plain southwest across the Sierra Nevada to the Pacific coast drainage (Stokes, 1979). Later, the Lahontan Basin (which still drained to the Pacific Ocean) was connected to the Snake River Plain. At different times, the White River (Hubbs and Miller, 1948b), Las Vegas Creek (Haynes, 1967), Death Valley–Owens River systems (Miller, 1946a, 1948), and perhaps even the Bonneville Basin (Ives, 1948) and upper Snake River were variously connected to the Bouse Embayment of the lower Colorado River. As the Sierra Nevada was uplifted, it is possible that a north-to-south drainage system included basins in Oregon and possibly Washington (Smith et al., 2000). There is good evidence that 2.5 million years ago (Ma) the Snake River's course changed with its capture by the Columbia River through Hell's Canyon (Wheeler and Cook, 1954). At undetermined times in the late Cenozoic, there were connections from the Mono Lake basin to the Lahontan Basin, from Owens River west to the Pacific coast drainage, and later, south to Mexico. In addition, Death Valley was connected to the lower Colorado River as well as to the Basin and Range Province in Mexico (Minckley et al., 1986; Hale, 1985). Fifteen to 20 thousand years ago (Ka) the basins of internal drainage were probably restricted mainly to northern and eastern Nevada and sometimes to the Death Valley system. At about that time, the Bonneville Basin and the basins of Catlow and Fort Rock Valleys and of Harney and Malheur Lakes (hereafter, Harney–Malheur) were sometimes tributaries to the Snake River (Taylor and Bright, 1987; Bisson and Bond, 1971; Minckley et al., 1986), whereas the White River was occasionally connected to the lower Colorado River (Taylor, 1983). The sizes and connections of basins fluctuated with climatic moisture through the late Pliocene (Smith et al., 1982) and the Pleistocene (Morrison, 1991; DiGuseppi and Bartley, 1991).

The hypotheses presented in this paper do not assume the above hydrographic outline, but they suggest that connections and disconnections, such as outlined above, were more frequent than commonly assumed. Our approach is to use fish fossils,

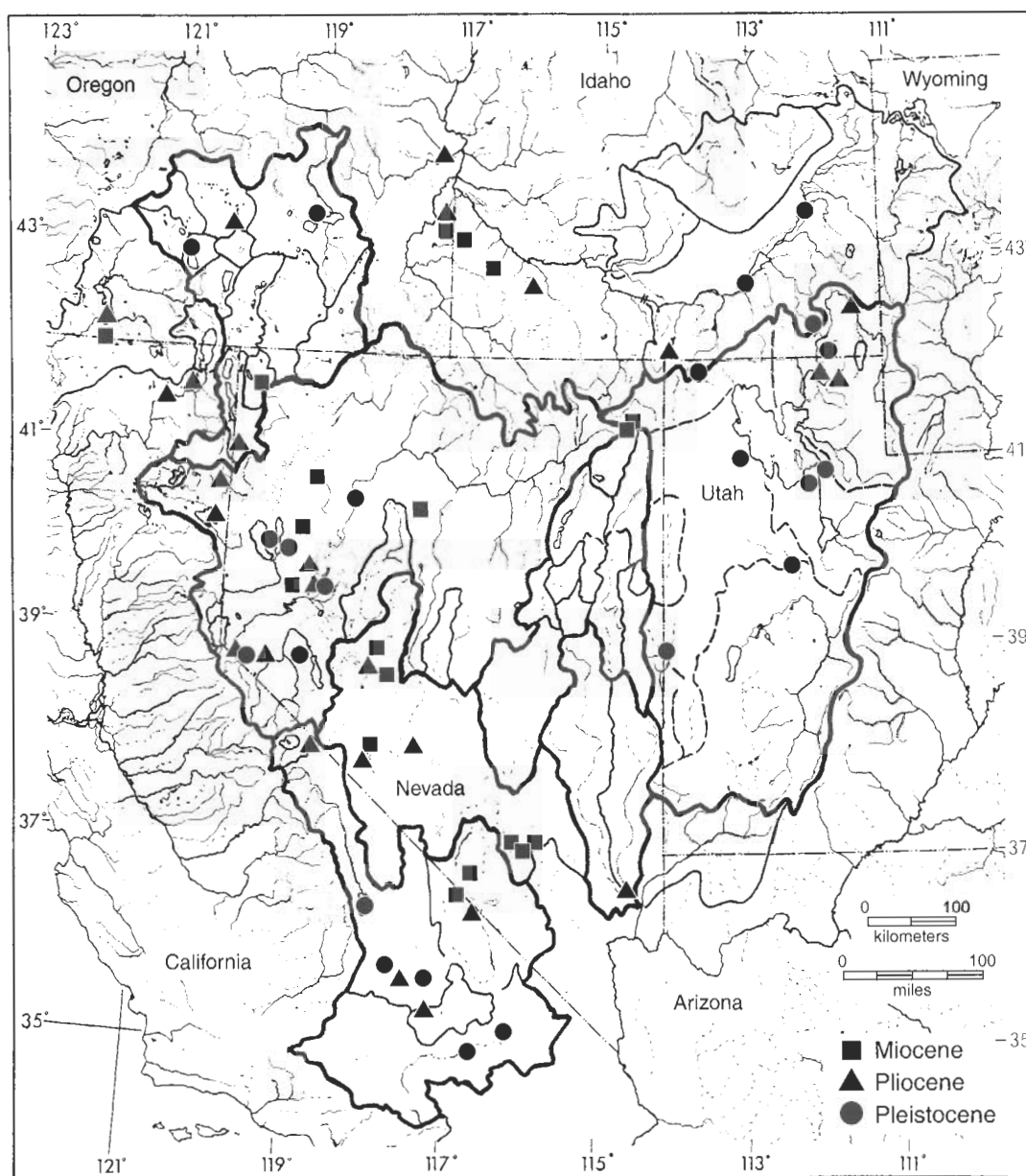


FIGURE 1.—Fossil fish localities in the Great Basin and adjacent drainages. Ages of fossil fish are indicated by symbols defined on the figure. Fossils are listed in the Appendix, where they are indicated by a cross. Heavy lines demarcate major drainage divides.

phylogenetic analysis, biogeography, and genetic distances as primary evidence for the times and locations of hydrographic change.

Material and Methods

Our hypothesized drainage connections are based upon distribution ranges of fish clades, species, or genetically similar populations, especially species and subspecies that span drainage divides that are no longer passable. We assume that ancient

fishes dispersed only through their habitats, because this method is supported by testable generalizations, in contrast to ad hoc hypotheses for dispersal of fish eggs, such as on birds' feet (e.g., Brown and Rosen, 1995; Spencer and Patchett, 1997). Likely geological mechanisms for transfer include lake spillover (Hubbs and Miller, 1948b), river capture, erosional beheading of streams, diversion of channels by erosion, and diversion of drainage by uplift or volcanic eruptions (Bishop, 1995). The degree of isolation of basins constrains dispersal, which leads to predictions that are testable by geographic, geo-

logic, genetic, and cladistic analyses. The large number of adjacent basins with similar habitats permits analysis of replicated histories of similar local faunas in addition to isolated case histories. It is important that we attempt to use fish data that are independent of geological assumptions, in the spirit of Hubbs and Miller (1948b) and Taylor (1960), so as to contribute non-circular conclusions useful to geology.

Records of Holocene fishes from the Great Basin were compiled primarily from the records of Hubbs (and his students and successors), which have been deposited in the Division of Fishes, Museum of Zoology, University of Michigan, and from the literature. Late Cenozoic fossil fish data (Figure 1; Table 1) were compiled from collections in the Museum of Paleontology and the Museum of Zoology, University of Michigan; the W.M. Keck Museum, Mackay School of Mines, University of Nevada, Reno; the Museum of Vertebrate Paleontology, University of California at Berkeley; the Department of Biology, California State University at Bakersfield; and the paleontological literature. (Lists of comparative material are available from authors G.R.S. and K.W.G.) Records of new distributions are noted in the species accounts in the Appendix. These accounts include information on specimen characteristics, collecting localities, and names of the collectors when the specimens were not deposited at the above-listed institutions (Appendix; Table 5). Ancestral-descendent pairs are recognized by shared apomorphies that are not shared with the next closest sister group. The probability of discovering ancestral-descendant pairs is thought to be low in marine and terrestrial systems (Foote, 1996), but in the Great Basin it is greatly enhanced by short geological time frame, highly constrained geography, the small number of taxa, and the salient osteological characteristics among fish taxa.

Cladistic methods used to estimate branching sequences for cyprinid fishes are from Dowling et al. (2002), Simons and Mayden (1997, 1998), and Cavender and Coburn (1992); for Catostomidae, Smith (1992b); for *Prosopium*, Smith and Todd (1993); for trout, Shiozawa and Evans (unpublished); and for Cyprinodontidae, Echelle and Dowling (1992). Molecular methods follow those used by Echelle and Dowling (1992), Shiozawa and Evans (1995), and Dowling and Naylor (1997). Cladograms were calculated from mitochondrial DNA (mtDNA) sequence data, using the parsimony algorithm "Phylogenetic Analysis Using Parsimony" (PAUP*; Swofford, 1990), version 4.0 d64 by D. Swofford. Informative characters among the species of Cyprinidae are the shared base pairs of the mitochondrial cytochrome *b* gene, relative to outgroups. North American and Eurasian cyprinids were used as outgroups for the analysis of western North American Cyprinidae. Informative cladistic characters among *Oncorhynchus clarki* and among *Cyprinodon* are shared restriction-site differences in mtDNA, relative to outgroups. *Oncorhynchus mykiss* (rainbow trout) is the outgroup for the cladistic analysis of subspecies of *Oncorhynchus clarki* (cutthroat trout). *Cyprinodon macularius* and several species of southwestern *Cyprinodon* from

outside the Great Basin served as outgroups for the cladistic analysis of *Cyprinodon* species of the Death Valley system.

DATA USED TO ESTIMATE THE RATE OF EVOLUTIONARY CHANGE PER UNIT TIME.—The relative homogeneity of molecular distances (Tables 2–4) among species with a common ancestor suggested a source of independent evidence to break the logical circularity inherent in using geological events to date evolution and in using evolutionary differentiation to date geological events. Previous workers carefully contrasted geological and ichthyological data, but it has been difficult to find independent data to constrain the time of geographic isolation. The traditional method (Hutchinson, 1939) defines a relevant interval of evolutionary time as beginning with the last possible period of hydrographic connection. This method assumes that one panmictic and homogeneous form at the time of connection evolved into two isolated and differentiated forms in the present. For example, it is assumed that a uniform Pliocene population before the Panamanian land bridge evolved into Pacific Ocean and Atlantic Ocean populations isolated by the Panamanian isthmus during the last 3.5 My (Bermingham et al., 1997). This method is limited to investigation of only one possible time for the origin of divergence, with bias toward the most recent.

It has been deemed parsimonious to choose the time of most recent connection as the beginning of the divergence because to choose an earlier time seemed to add an unnecessary ad hoc hypothesis, i.e., more time than is minimally necessary. Discovery of the amount of time required for the observed divergence is, however, the original question, and to assume the shortest of several possible times does not test the hypothesis. It is important to test the alternative possibility, namely, that multiple populations were present prior to the time of last connection and that the forms observed in the Holocene have been accumulating genetic differences for a time period longer than since the last connection. This alternative is important for studies such as the Panamanian separation of Atlantic and Pacific marine faunas, as well as for freshwater fishes in the Great Basin. Divergence times of clades must ultimately be based upon ages determined from the stratigraphic context of fossils—usually some combination of mammalian biostratigraphy (Woodburne, 1987), potassium–argon, ^{40}Ar – ^{39}Ar , or other radiogenic dates (e.g., Baksi et al., 1992), magnetostratigraphy (Negrini et al., 1987), fission-track ages (Kimmel, 1982), and field studies of geomorphology and geochemistry (e.g., Allison, 1940, 1982; Hubbs and Miller, 1948b; Bright, 1966, 1967; Benson and Thompson, 1987; Benson et al., 1990; Curry, 1990; Morrison, 1991; Reheis and Morrison, 1997).

We compared data on divergence of mtDNA molecules among fishes (Kocher and Carleton, 1997) with dates of relevant fossils to calculate rates of molecular evolution (Collins et al., 1996). Molecular differences among homologous mitochondrial genes in these taxa are expressed as pairwise percent sequence divergence (Gillespie, 1991). The difference values are proportions of the specified part of the genome that differ in

TABLE 1.—Late Cenozoic fossil fish localities in the Great Basin. Numbers refer to indexed taxa mentioned in the Appendix; a question mark (?) = uncertain identification or age.

Locality, by state	Indexed taxa	Source ¹
MIOCENE		
Nevada		
Bullfrog Mine near Beatty, Nye County, 23 Ma?	117	Lugaski, UNRM
Esmeralda, Esmeralda County	5, 27, 28, 58, 88, 120	LaRivers, 1962, UNRM
Siebert Tuff, Nye County, 17 Ma	122	Lugaski, 1978, UNRM
Buffalo Canyon, Churchill County, 15 Ma	6, 88	T. Lugaski, UNRM
Middlegate Formation, Churchill County	88	D.I. Axelrod, UCD
Stewart Valley, Mineral County, 12 Ma	27, 88	
Virgin Valley, Humboldt County	6, 58, 124	Lugaski, UNRM
Truckee Formation, Churchill County	8, 29, 80, 89, 128	Bell, UMMP
Red Rock locality, Churchill County	87	J.R. Alcorn, UMMP
Rabbit Hole, Pershing County	88	LaRivers, UNRM
Sahwave Mountains, Pershing County	116, 128	
Humboldt Formation, Elko County, 9.5 Ma	123, 130	Lugaski, UNRM
Coal Valley, Mineral County	6, 88	T. Kelly, MVP
Alum Mine, Nye County	88	LaRivers, UNRM
Jersey Valley, Pershing County	8	Lugaski, UNRM
Brady Pocket, Churchill County, Hemphillian?	56	Charles Dailey, MVP, UMMP
Carson Valley, Douglas County	15, 30, 88	
Oregon		
Trout Creek, Harney County	129	C. Arnold, UMMP
Utah		
Cache Valley Formation, Salt Lake group	3	J.S. Williams, USU
PLIOCENE		
California		
Secret Valley, Lassen County	1, 30, 69, 91, 124	UMMZ, Wagner et al., 1997, MVP
Madeline Plains, Lassen County	1, 25, 26?, 30, 91	Wagner et al., 1993, MVP
White Hills, Airport Lake, Inyo County	12, 62	Gobalet, UMMP
Mono Basin	1, 13, 14, 30, 63, 74	Miller and Smith, 1981; Gobalet, UMMP
Honey Lake	9, 25, 60, 65, 68, 70, 91	Taylor and Smith, 1981, UMMP
Idaho		
Salt Lake group at Georgetown	3, 59	S.A. Bilby, ISU
Nevada		
Carson Valley, Douglas County, early Blancan	2, 15, 30, 64, 75	T. Kelly, Gobalet, MVP
Carson Valley, Douglas County, late Blancan	2, 15, 64, 92	T. Kelly, Gobalet, MVP
Pine Nut Ridge, Douglas County	6	T. Kelly, 1994, MVP
Duck Valley, Washoe County	10, 62	
Carson Sink, Churchill County	92	
Mopung Hills, Churchill County	9, 72, 93, 124	Taylor and Smith, 1981, UMMP
Fish Cave, Churchill County	124	R. Miller, UMMP
Oregon		
Fort Rock Lake, Lake County, Blancan	7, 59, 62, 90	Allison and Bond, 1983, OSU
Utah		
Junction Hills, Salt Lake group, Hemphillian	3, 23, 26, 30, 57, 61, 69, 81	P. McClellan, MVP
Park Valley, Box Elder County, Hemphillian?	125	T. Cavender, UMMP
PLEISTOCENE		
California		
Manix Lake, San Bernardino County	12, 129	Buwalda, 1914; Reynolds, 1991, 1994
Searles Lake, San Bernardino County	12	
China Lake, San Bernardino County	12, 62	UMMP
Lake Mohave or Soda Lake, San Bernardino County	12	Leatham, UMMP
Owens Lake Core, Inyo County	13, 73, 82, 92	G.I. Smith, UMMP
Nevada		
Humboldt River Canyon, Pershing County	10, 92	Gobalet, MVP
near Fallon, Churchill County	60, 72	J.R. Alcorn, UMMP
Carson Valley, Irvingtonian	15, 30, 64	T. Kelly, Gobalet, MVP
Sunshine Amphitheater, northwestern Walker Lake, pre-Lahontan	72, 92	M. Reheis, USGS
Lahontan Cave deposits	124	Jordan, 1924, MVP
Smith Creek Cave	23, 99	Mead et al., 1982

TABLE 1.—Continued.

Locality, by state	Indexed taxa	Source ¹
Oregon		
Chewaucan, Lake County	11	Gobalet and Negrini, 1992
Utah		
Hot Springs, Salt Lake County	23, 66, 84, 85, 125, 126	Smith et al., 1968, UMMP
Black Rock, Salt Lake County	23, 84, 85, 98, 125, 126	Smith et al., 1968, UMMP
Black Rock, Tooele County	23	J.H. Madsen, Jr., UMMP
Homestead Cave	23, 66, 84, 85, 87?, 98, 126	Broughton, UU
Thatcher Basin	61	Bright, UMMP
Old River Bed	62, 82, 98	Oviatt, UU
STRATIGRAPHY UNCERTAIN		
Nevada		
Nevada AEC Test Site, Nye County, Miocene?	119	Richard Wyman, UMMP
California		
Titus Canyon, Pliocene? (stratigraphy uncertain)	111, 117	Miller, 1945b
Titus Canyon Formation, Oligocene?	117	Lugaski, UNRM
Furnace Creek, Death Valley, Pliocene?	118	Miller, 1945b

¹Published source and/or collector and location of specimens. Abbreviations: ISU = Idaho State University Museum, Pocatello; MVP = Museum of Vertebrate Paleontology, University of California, Berkeley; OSU = Oregon State University, Corvallis; UCD = University of California, Davis; UMMP = University of Michigan Museum of Paleontology, Ann Arbor; UMMZ = University of Michigan Museum of Zoology; UNRM = Mackay School of Mines, University of Nevada, Reno; USGS = United States Geological Survey; USU = Department of Geology, Utah State University; UU = University of Utah.

accumulated mutations, corrected for back mutation (Tamura and Nei, 1993). We were encouraged to pursue this method by the homogeneity of values of pairwise comparisons of sets of lineages, each derived from a common ancestor (Tables 2–4). This homogeneity suggested that the rate of molecular evolution was roughly constant for a given gene system in a given clade. The relative-rate test of Sarich and Wilson (1967) was used to evaluate the precision of the time estimate. It is based upon the assumption that all taxa derived from one node (branch point) on a cladogram have evolved while accumulating mostly neutral mutations for the same amount of time (e.g., Figure 2; Table 2), regardless of the number of intervening branch points; therefore, all the distances (in a homologous molecule) from the sister clade to all the members of the clade in question should be identical. This degree of similarity is a measure of the constancy of the rate of molecular change and, therefore, an estimate of the precision of a molecular estimation of geological time. In other words, the homogeneity of the measured distances between sister branches within a clade is an indication of how constant the rate of molecular change has been. It is important to stress that these distance values were tested in conjunction with ages of fossil fish that we interpret as ancestors; distance values were not converted to rates of molecular change based upon molecular clock assumptions from mammals or other organisms.

If we accept the accumulated differences (genetic distance) as numerators in a rate estimate for these fishes, we then need an independent denominator measured in millions of years to yield the amount of molecular change per one million years (Collins et al., 1996). The denominator, evolutionary time, is

estimated herein as millions of years since the time from first appearance of a fish lineage to the present. Relative times of lineage origins, recognized by possession (in fossils) of evolutionarily derived states that diagnose appropriate groups (Lundberg, 1993), are underestimated because occurrences of fossils are usually minimum estimates of the age of their lineage (Minckley et al., 1986). This problem exists because the first members of a lineage are not only rare, they are also not easily recognized (assuming that apomorphies accumulate gradually at many points along branches between nodes). Where fossils are limited to infrequently preserved depositional environments, the sample sizes are not adequate to evaluate statistical error around the estimated age of the first occurrence of a lineage. The denominator error from underestimated times of first appearance results in overestimated rates of change (rate = percent divergence/time). Errors in the numerators, e.g., from back mutations, yield underestimated rates, unless genetic distances are adequately corrected (Tamura and Nei, 1993). The potential consequences of these errors are readily apparent from inspection of Figure 14, in which numerator error is corrected, but denominator error is not; therefore, our rates of molecular change (0.5%–1%/My) are likely to be overestimates, approximating upper bounds. If the oldest of these lineages are as old as the Oligocene, as suggested by Minckley et al. (1986), correct rate estimates could be 0.3%–0.7%/1 My.

The pairwise difference values for lineages in a clade, such as the Cyprinodontidae, Salmonidae, or Cyprinidae, are regressed against geological divergence-time estimates (Figure 14). The regression coefficient then gives the percent sequence

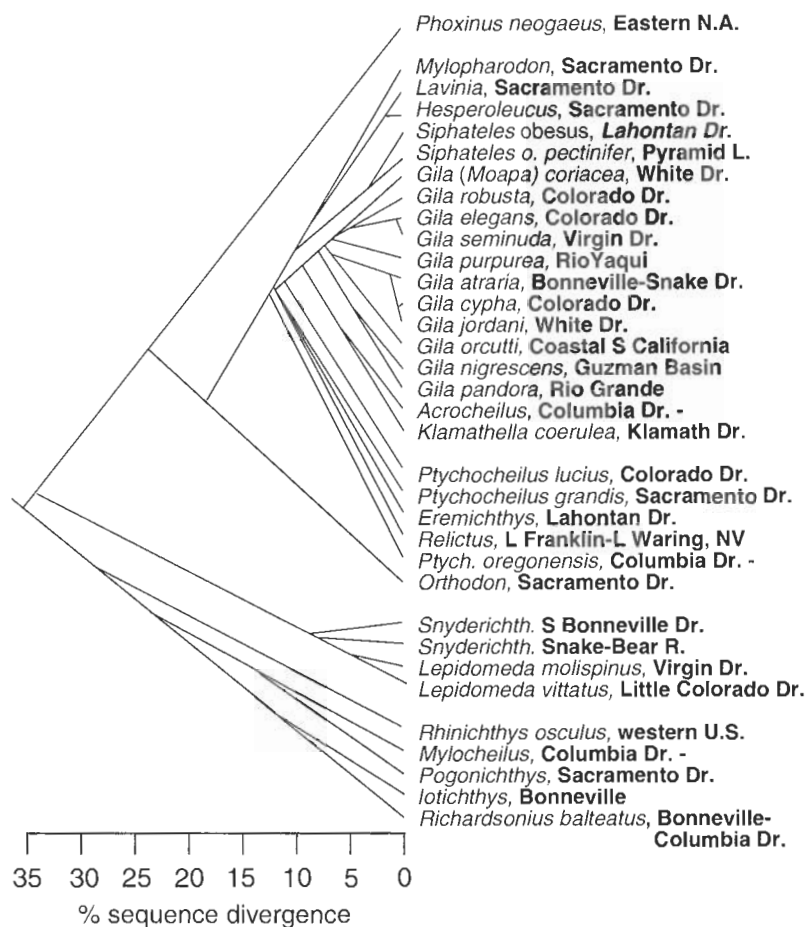


FIGURE 2.—Mitochondrial DNA phylogeny of western Cyprinidae, based upon parsimony cladistic analysis of the cytochrome *b* gene. This tree is extracted from a larger analysis of 88 cyprinid taxa (Dowling, unpublished). The relative rates test (see "Methods") is based on the expectation that all of the sister species to any outgroup should have the same percent sequence divergence. The variation in those distances (Tables 2–4) is a measure of the variation in relative rates of change and the lack of precision in any inference. The depth to each node is scaled to age in millions of years, assuming that 1 My corresponds to 1% average distance between clades (Table 2). Rank order of cladistic nodes and distances is preserved within 1%, except that the *Relictus*–*Eremichthys* distance is 15%.

divergence per one million years for that gene and that clade (Figure 14), with an indication of the reliability of that estimate (Table 2). Once we have estimated the rate of change for a gene in a taxon, we can return to the cladogram and can estimate the amount of absolute time elapsed between sister clades in different basins, as estimated by genetic differences. Cladograms (without time) can then be recast as phylogenies (with estimates of time), as in Figures 2, 10, and 11. The estimated rate depends upon the correction factor for back mutations at all base pair sites. For example, the Tamura–Nei correction, used herein, gives 50 percent higher sequence-divergence values and older branch times (for the older cyprinids) than *p* distances or the Kimura two-parameter correction (Tamura and Nei, 1993).

In the analyses below, both morphological and molecular cladistic estimates of rates of change are presented for the Cyprinidae (Figures 2, 3), but the molecular cladistic estimate is used to frame the relative-rate test. Correlations between the node sequences of the molecular trees and percent sequence divergence are positive and significant; correlations between node sequences of the morphological trees and percent sequence divergence are not significant.

Different kinds of hydrographic connections between basins affect molecular-rate estimates differently. For example, lacustrine spillovers of lakes into rivers that transferred low-elevation suckers, minnows, pupfishes, lacustrine trouts, and whitefishes occurred in sometimes datable pluvial times during

glacial cycles (e.g., Lake Bonneville's spillover, McCoy, 1987), but headwater stream captures that transferred cold-water, high-gradient mountain suckers, salmonids, and sculpins occurred more frequently (e.g., between the Bear, Snake, and Green Rivers). Therefore, large, lowland fishes will generally contribute to older time estimates, whereas headwater fishes contribute to younger estimates. This is independent of the question of whether headwater fishes evolve more rapidly (Smith, 1992b).

There are two alternative general hypotheses for times of divergence of Great Basin fishes. The first alternative is that a population was devoid of genetic structure prior to the most recent connection. Alternatively, differentiation may date not from the most recent connection and disconnection, but from a previous period of high water in the Pleistocene or Pliocene (see discussions of Whitehorse and Bonneville cutthroat trout and Death Valley pupfishes, below). Consideration of a broader range of possible isolation phenomena, along with dated fossils and molecular data, enable us to test alternative hypotheses about timing of divergence.

Several additional problems may detract from the generality of these methods. In particular, fish fossils are limited, and some possess few apomorphic characters. More complete molecular cladograms for more taxa are also needed. In addition, mtDNA data may have suffered introgressive loss of evolutionary information in basins that frequently changed connections

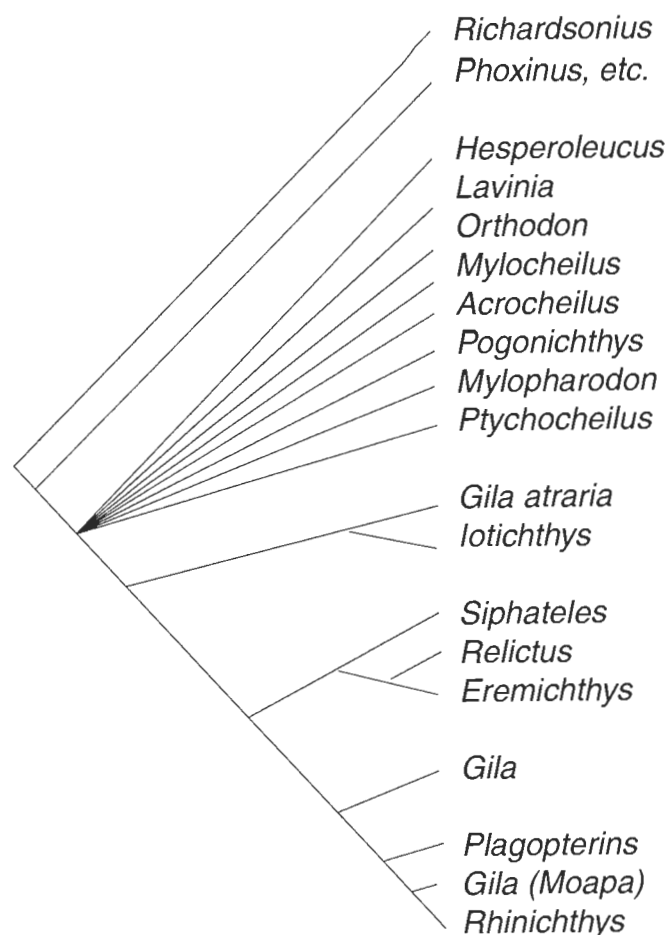


FIGURE 3.—Morphological phylogeny of western Cyprinidae after Coburn and Cavender (1992). This tree was extracted from a consensus tree, which was based upon 100 equally parsimonious trees representing a larger sample of cyprinid fishes.

among allopatric populations (Smith, 1992a; Echelle and Dowling, 1992; Dowling and Secor, 1997).

Cladistic patterns and estimated amounts of molecular divergence are presented in the "Results." Distinct population units are listed and indexed in the Appendix, with their diagnostic characters, location, fossil ages, and brief history. Statements about the kinds of characters and the qualitative degree of differentiation seen between sister units are included to enable comparisons with our molecular- and fossil-based hypotheses about rates of evolution.

Authors of recent species and subspecies names are given in the Appendix, following Robins et al. (1991). Citations and authors of species names of fossils are given in the Appendix. Institutional abbreviations are defined in Table 1.

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Robert Miller and his family and students collected thousands of fossil fish bones. Dwight W. Taylor was important in

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Results

Fifty-two recent species—19 Cyprinidae, 12 Catostomidae, eight Salmonidae, five Cyprinodontidae, four Goodeidae, and four Cottidae—comprise the Holocene Great Basin fish fauna. Twenty-seven of these species are endemic. Four species among the cyprinids, goodeids, and cottids have been driven to extinction, and two species or subspecies of salmonids have been extirpated from the Great Basin as a result of habitat destruction caused by human activities (Minckley and Deacon, 1991). Among the 52 species (especially cyprinids, salmonids, and cyprinodonts), more than 50 additional isolated populations have been recognized as separate subspecies. Sixty-four fossil forms, from the late Miocene to the present, represent many recent lineages and several clades that are now locally extinct (for example, Gasterosteidae and Centrarchidae). Fossil

fishes are now known from 55 Great Basin localities (Figure 1; Table 1); several hundred additional fossil localities occur at the northern edge of the Great Basin, on the Snake River Plain. Extensive analyses of mtDNA divergence have been carried out on recent representatives of these fossil forms: Dowling et al. (2002) on Cyprinidae (minnows), Echelle and Dowling (1992) on Cyprinodontidae (pupfishes), and Shiozawa and Evans (1995) on Salmonidae (trouts).

CYPRINIDAE.—Minnows, family Cyprinidae, are the most diverse and widespread fishes in the Great Basin; the 19 Holocene lineages include 10 endemic species and more than 20 endemic subspecies. Three species of minnows, *Gila atraria*, *Siphateles bicolor*, and *Rhinichthys osculus*, have been especially persistent and have differentiated into many distinct subspecies and local populations. Unfortunately, small minnows are under-represented in the Great Basin fossil record, so they contribute little to our estimates of rates of molecular evolution. At least five lineages, *Ptychocheilus*, *Mylocheilus inflexus*, *M. robustus*, *Mylopharodon*, and *Lavinia* (exclusive of *Hesperoleucus*), lived in the Great Basin in the Pliocene and Miocene but are absent there today. *Siphateles* is the best represented genus in the fossil record, occurring in the Miocene to Pleistocene of the Lahontan Basin and Mohave River drainages.

Fossil and living Cyprinidae in the Great Basin are herein assigned to three ancient clades, which are based on our molecular analyses (Figure 2; see also Simons and Mayden, 1997, 1998). These three clades are older than the Great Basin, and molecular evidence indicates that they probably date back to the Oligocene (Table 2; Appendix). The first of the three clades (Figure 2) in the Great Basin (including fossils) is the large western North American chub group that includes *Mylopharodon*, *Lavinia*, *Hesperoleucus*, *Siphateles*, *Gila*, *Acrocheilus*, *Klamathella*, *Ptychocheilus*, *Eremichthys*, and *Relictus* (Appendix, numbers 1–32). These are related to *Orthodon* in the Sacramento drainage system and to *Phoxinus* in eastern North America. This “Western Chub clade” has four subgroups in the Great Basin: (1) the *Mylopharodon*–*Lavinia*–*Hesperoleucus* and *Siphateles* clade (Appendix, numbers 1–22); (2) the *Gila*–*Acrocheilus*–*Klamathella* clade, with *Ptychocheilus lucius* as its sister group (Appendix, numbers 23–29); (3) the *Relictus*–*Eremichthys* clade, including *Ptychocheilus grandis* (Appendix, numbers 31–32); and (4) the *Ptychocheilus oregonensis* clade (Figure 2; Appendix, number 30). Whether or not *Ptychocheilus* is actually paraphyletic, as indicated by Figure 2, is problematical. *Ptychocheilus* cf. *oregonensis* is one of the oldest cyprinids in the region (Smith et al., 2000).

The second major cyprinid group in the Great Basin is the *Snyderichthys*–*Lepidomeda* (spinedace) clade (Appendix, numbers 33–35). It is related to the other spinedaces, which inhabit tributaries of the Bouse Embayment (see below). Sister groups of this clade include *Margariscus* and *Couesius* of northern and eastern North America.

The third major minnow clade includes western American outliers of the huge eastern North American shiner clade. Western forms include *Iotichthys* (Appendix, number 36), *Richardsonius* (Appendix, numbers 37–39), *Rhinichthys* (Appendix, numbers 40–55), and *Mylocheilus* (Figure 2; Appendix, numbers 56–58). This group also includes *Pogonichthys* of the Sacramento drainage system. An alternate cladistic hypothesis (Figure 3), based upon morphological analysis, shows different interpretations of relationship (Coburn and Cavender, 1992).

Great Basin cyprinids are listed (Tables 1, 2), numbered, and reviewed in the Appendix in approximately the sequence given in Figure 2. Typical distribution patterns of minnows (illustrated by *Gila* and *Siphateles*) are shown in Figure 4.

Fossil minnows in the Great Basin date back to the middle Miocene or earlier (Cavender, 1986; Reynolds, 1994). Many cyprinid genera are early members of the Great Basin fauna (Appendix, numbers 5, 14, 15, 26–28, 30, 56–58). The *Gila* group is widespread and especially diverse in all of the Great Basin as well as in the Colorado River drainage, the Rio Grande, and northern Mexico. *Siphateles* is centered in the Lahontan Basin and Sacramento River drainages, and *Gila* is in the drainages surrounding the Lahontan Basin. The Great Basin part (White River) of the lower Colorado River (Bouse Embayment) drainage is inhabited by *Lepidomeda*, *Moapa*, and *Gila*, as well as by *Catostomus clarki* and the empetrichthyine good-eids. *Snyderichthys copei* of the Bonneville Basin and upper Snake River drainages is cladistically part of the Plagopterin group and provides evidence of Pliocene and Pleistocene drainage connections (Dowling et al., 2002). The southern California coastal form, *Gila orcutti*, is the sister group to *Gila atraria* of the Great Basin and to *G. jordani* and *G. cypha* of the Colorado River drainage.

Electrophoretic variation in *Gila atraria* of the Bonneville Basin was studied by Rosenfeld (1991), who concluded that accumulated differences were influenced more by natural selection in local springs, lakes, and streams than by vicariance and time. He estimated that 14,500 years was too short an interval for the accrual of qualitative differences between hierarchical groups of vicariant populations. Populations of *Gila atraria* from northern and southern Bonneville basins and from the Bear River have diverged extensively in their mtDNA; they have not remained uniform during the last 2 My (sequence divergence = 0.009–0.024) despite recent and probably frequent sympatry. The northern Bonneville form of *G. atraria* shares an unexpectedly high proportion of its mtDNA with *G. cypha* and *G. jordani* of the Colorado River (percent sequence divergence = 1.1% and 0.7%, respectively; Table 2), supporting the hypothesis that a connection existed from Lake Bonneville through Meadow Valley Wash, Nevada, to the Colorado River drainage (Ives, 1948).

A separate biogeographic pattern encompasses the northern Great Basin and the Columbia River and Snake River drainages. This pattern is marked by the distributions of *Klamathella*, *Siphateles*, *Acrocheilus*, *Lavinia*, *Mylopharodon*, and

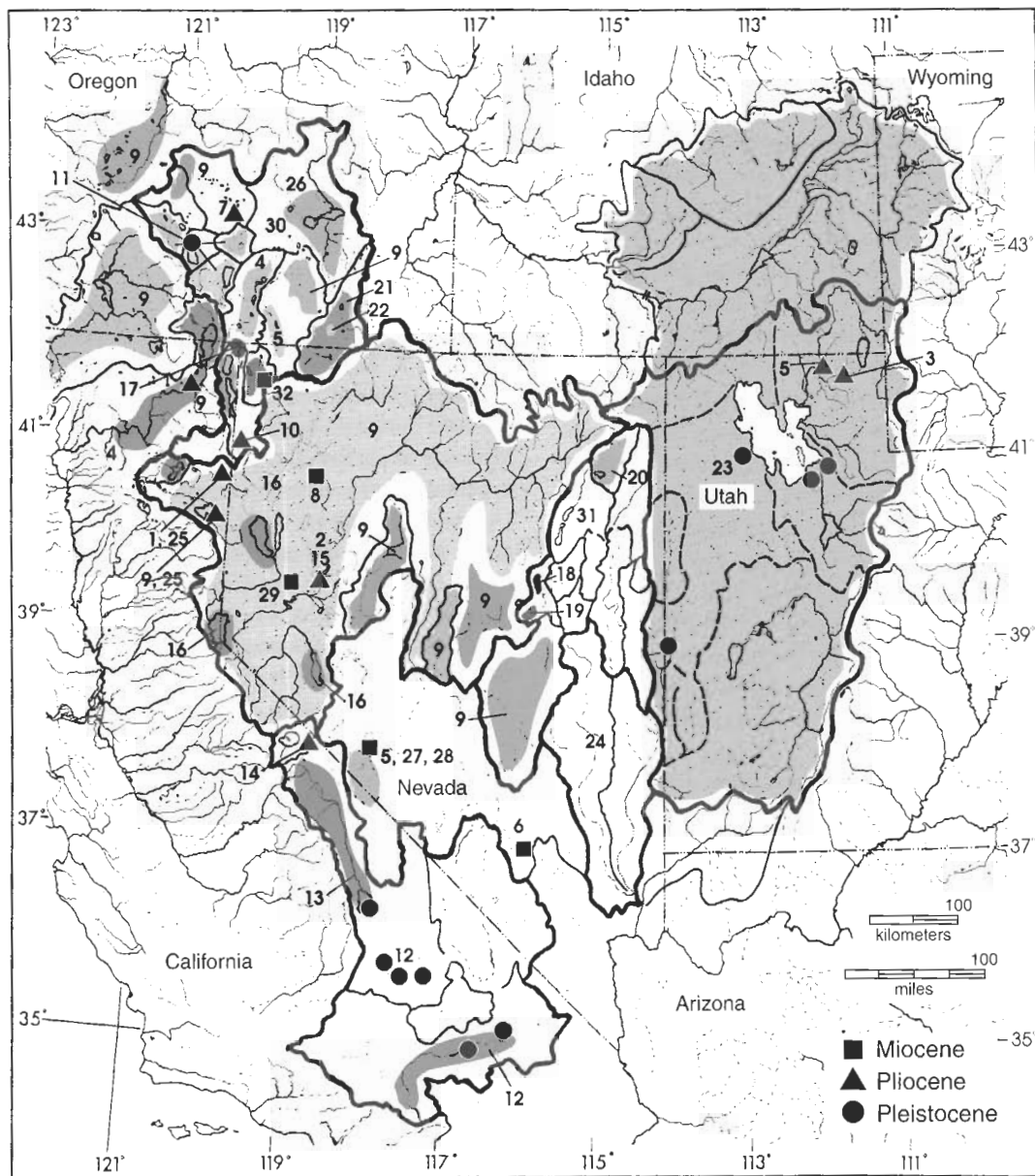


FIGURE 4.—Distribution of Holocene and fossil *Siphateles*, *Gila*, and certain relatives in the Great Basin. Map shading indicates different species or subspecies ranges. Ages of fossil fish are indicated by symbols defined on the figure. Numbers refer to species or subspecies listed in the Appendix.

Mylocheilus in a Columbia–northern Great Basin–Pit River track. At a lower cladistic hierarchical level, this biogeographic pattern broadens to include the Sacramento River drainage, with *Ptychocheilus grandis*, *Hesperoleucus*, and *Orthodon* (Figures 2, 3), and the Colorado River drainage, with *Ptychocheilus lucius*. The several Great Basin records of *Mylocheilus* and *Mylopharodon* are evidence of a late Miocene connection between west-central and northwestern Nevada and the Snake River Plain. *Mylocheilus caurinus* (Table 2, number 58) is the closest living relative to *Mylocheilus robustus* of the Mio–Pliocene Snake River Plain (Appendix, number 58) and to

Mylocheilus heterodon from the Ringold Formation of Washington (Smith et al., 2000).

Pairwise distances among clades that are based upon a parsimony cladistic analysis enable evaluation of relative rates of molecular change (Table 2). The homogeneity of these rates among minnows can be evaluated by comparing the standard deviation (s.d.) around the mean distances. The 26 species estimated to share a common ancestor with *Phoxinus* have a mean distance between each of them and *Phoxinus* of 0.22 (s.d. = 0.022). The 66 combinations of sister species to *Mylopharodon*, *Lavinia*, and *Hesperoleucus* have a mean distance of 0.15

(s.d. = 0.02); the 38 combinations of *Siphateles* sister species have a mean distance of 0.12 (s.d. = 0.02); the 30 species of the *Gila orcutti*–*G. atraria* group have a mean distance of 0.08 (s.d. = 0.02); the 26 sister species to *Acrocheilus* and *Klamathella* have a mean distance of 0.08 (s.d. = 0.02); the 216 combinations of the spinedaces have a mean distance of 0.34 (s.d. = 0.03); and the 210 combinations of the western representatives of the shiner clade have a mean distance of 0.35 (s.d. = 0.05). With the rate of divergence estimated at about 1% per one million years, the standard deviations of group or barrier ages is usually on the order of 10%, but rarely more than 25%, of the estimated age (Table 2). The distances and inferred

timing of cyprinid patterns span the time from Miocene to the last postpluvial period.

CATOSTOMIDAE.—Catostomids are the most ancient of the fish groups present in the Great Basin (Cope, 1872; Smith, 1966, 1992b; Minckley et al., 1986). They are also among the largest and hardiest aquatic survivors of the Great Basin's historically variable climate and ecology. Catostomidae are the second most diverse and abundant family in the Great Basin, with 12 species, but the maximum number of sympatric forms is three or four. Great Basin suckers are part of a primarily western American monophyletic group (Figure 5), the Catostomini, whose sister group (and outgroup in the analysis) is the

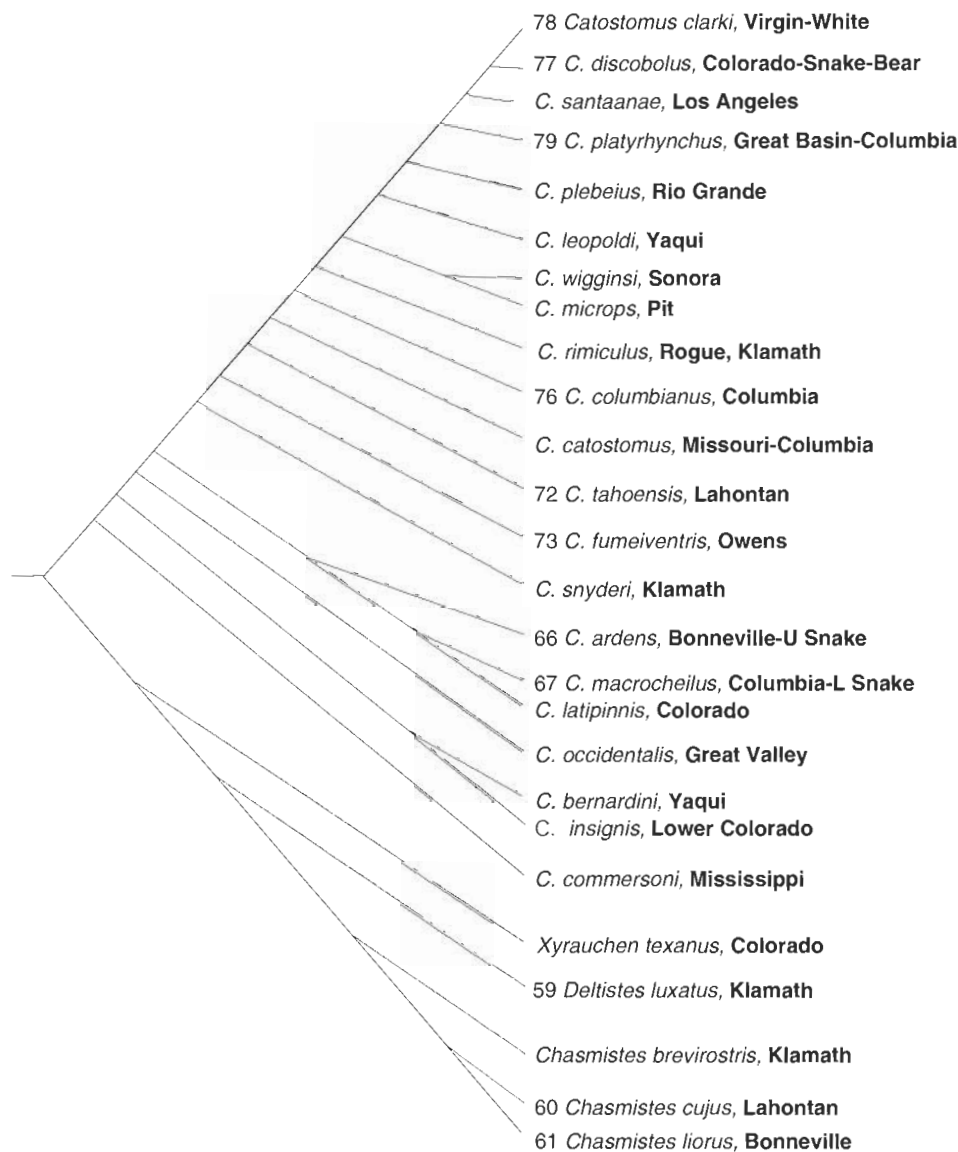


FIGURE 5.—Estimate of the phylogenetic tree for *Chasmistes*, *Deltistes*, and *Catostomus* in the Great Basin and their relatives in the Catostomini (from Smith, 1992b). Not all species of *Chasmistes* were included in the cladistic analysis. Numbers refer to the species accounts in the Appendix.

Moxostomatini of the eastern United States and Mexico (Smith, 1992b).

The Catostomini range from medium-sized, benthic, head-water species in the subgenus *Pantosteus* (genus *Catostomus*) (Figure 7), to large-sized benthic predators in low-gradient streams (other *Catostomus*, Figure 6), to large-sized planktivores in large lakes (*Chasmistes*, Figure 7). The fossil record of catostomids is diverse; it includes plesiomorphic forms as well as forms that were morphologically more specialized than present-day species. Fossil *Catostomini* are known from the

Miocene (10 Ma) to the Holocene, with Great Basin diversity reaching a peak of four species in the northern Bonneville Basin (and upper Snake River and upper Colorado River basins) in the late Pleistocene (see Appendix, numbers 59–79). Catostomids are tetraploid fishes that show abundant hybridization and extreme variation, but no indication of rapid speciation (Smith, 1992b).

There are two clades of Catostomini in the Great Basin (Smith, 1992b). The first is the genus *Chasmistes*, the lake suckers. Four Holocene species of *Chasmistes* are localized in Utah

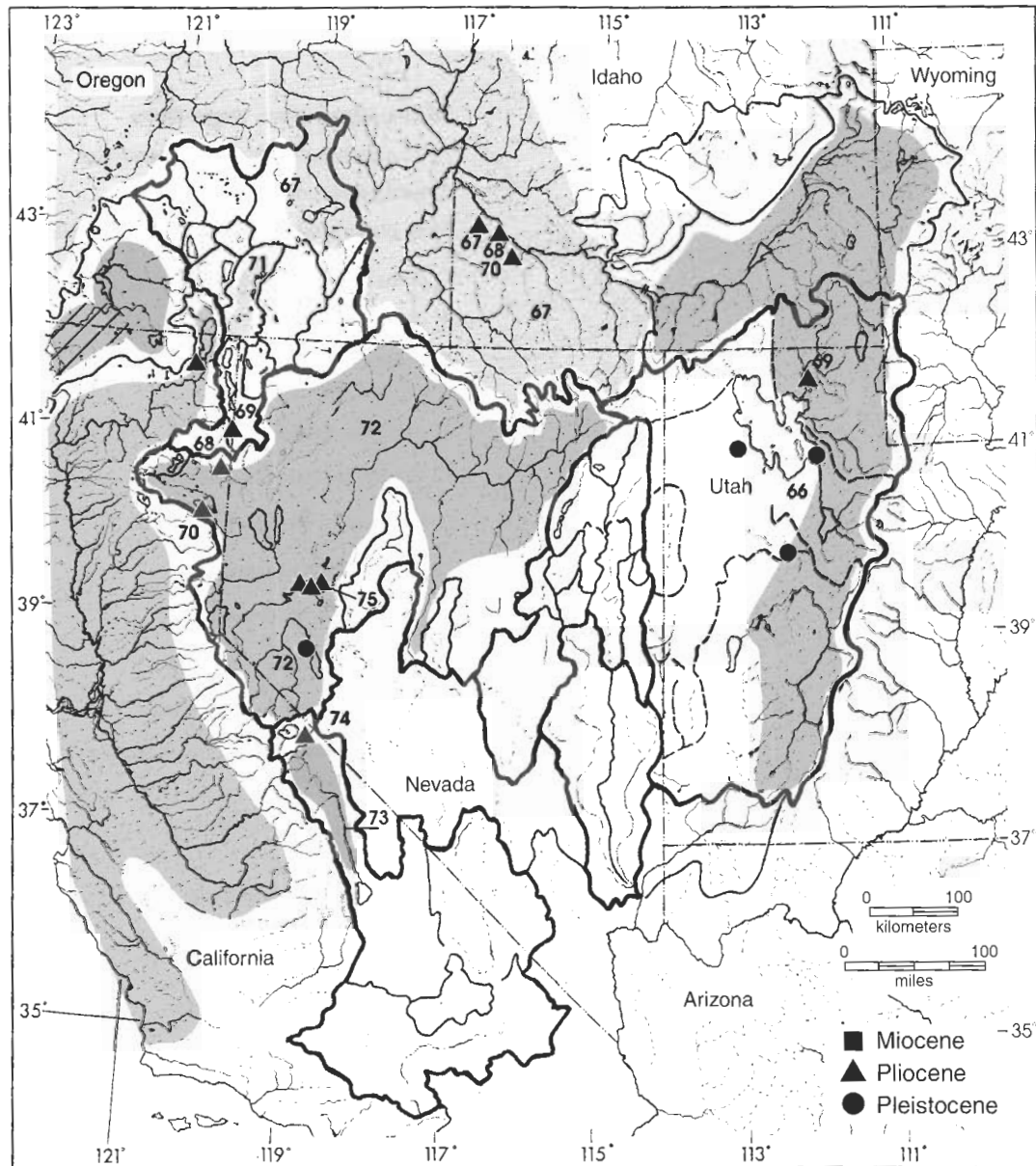


FIGURE 6.—Native distribution of *Catostomus ardens* (Utah, 66), *C. macrocheilus* (Idaho, 67), *C. fumeiventris* (southern California, 73) and *C. tahoensis* (Nevada, 72) in the Great Basin and some of their relatives outside the Great Basin. Shading indicates drainage basins occupied by species (as numbered in the Appendix). Fossil records and Holocene occurrences are indexed to the numbered species accounts in the Appendix. Ages of fossil fish are indicated by symbols defined on the figure. These are low-gradient fishes that required a major river or lake connection to cross a drainage divide.

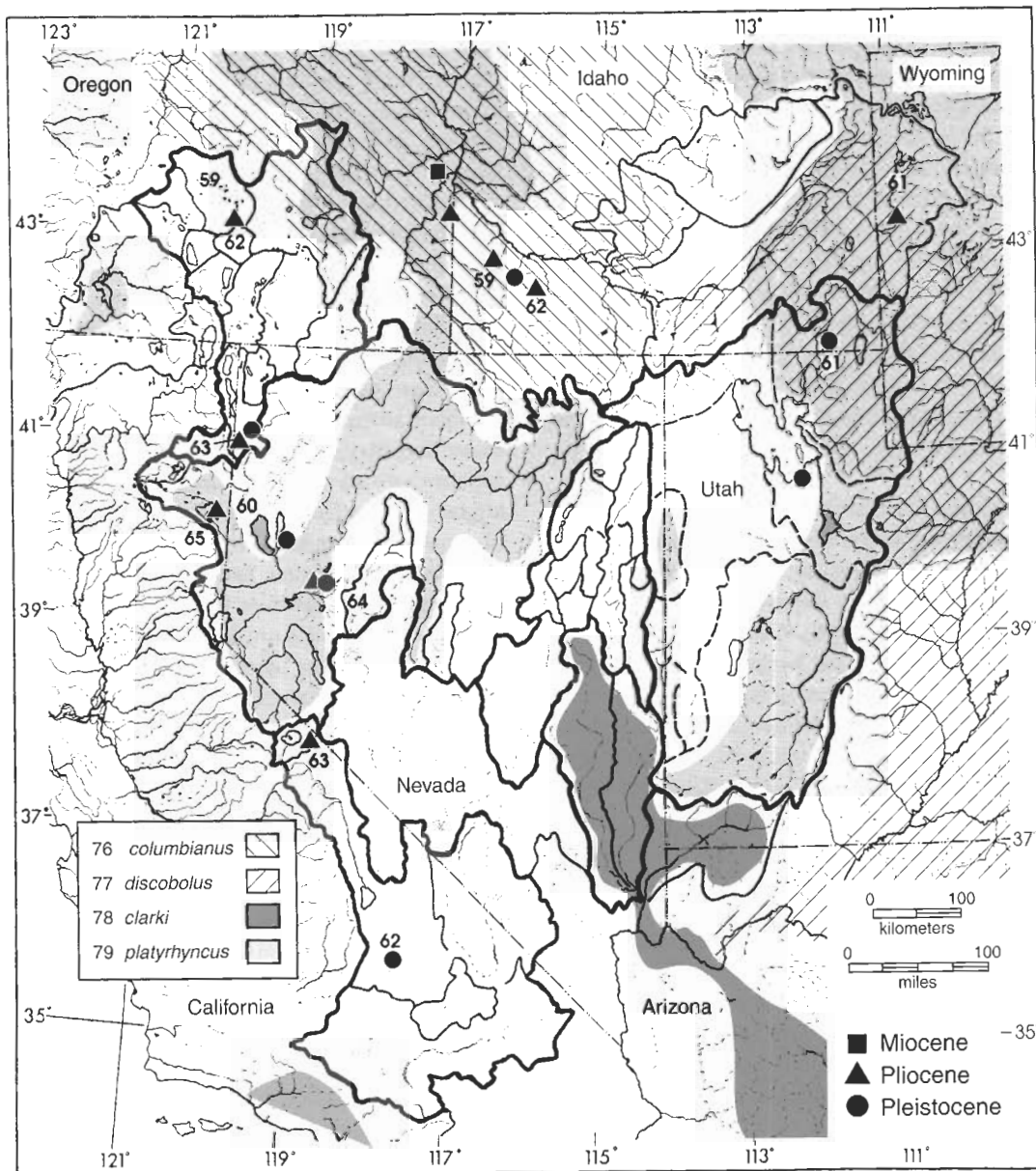


FIGURE 7.—Distribution of the mountain suckers: *Catostomus platyrhynchus* (Utah, Idaho, Wyoming, Nevada, 79), *C. columbianus* (Idaho, Oregon, 76), *C. clarki* (southern Nevada, 78), and *C. discobolus* (Utah, Wyoming, Idaho, Colorado, 77) in the Great Basin and of their relatives (*C. rimiculus*, Oregon; *C. santaanae*, California) outside the Great Basin. Ages of fossil *Chasmistes* and *Deltistes* in the Great Basin are indicated by symbols defined on the figure. Numbers refer to the species accounts in the Appendix.

and Pyramid Lakes, in Klamath River (Figure 7), and in the headwaters of the Snake River. There are also numerous Miocene to Holocene fossil *Chasmistes* specimens in the Great Basin (Miller and Smith, 1981; Figure 7). Silicified gill-raker plates with fimbriate distal ends have been found in the Mono Lake basin. Fimbriate distal ends are an apomorphy for *Chasmistes*. Their presence in Mono Lake deposits indicates this adaptation to planktivory occurred 4–3 Ma (Gobalet, unpublished data). The sister genera to *Chasmistes* are *Xyrauchen* and *Deltistes*

(Appendix, number 59) of the Colorado River and the Klamath system, respectively. The modern lake sucker in Utah Lake, *Chasmistes liorus mictus* Miller and Smith (1981), shows intense introgression from *Catostomus ardens*. The introgressive event is remarkable because *Chasmistes* and *Catostomus* diverged 10–4 Ma (both genera are morphologically distinct in Pliocene sediments of the Snake River Plain; Smith et al., 1982).

The second clade is the genus *Catostomus*, which includes two ecological groups that were formerly classified as subgenera

(Smith, 1966; Smith and Koehn, 1971). As now understood, the subgenus *Pantosteus* (mountain suckers) (Appendix, numbers 76–79) is monophyletic, but recognition of *Pantosteus* makes the subgenus *Catostomus* paraphyletic (Smith, 1992b). The more plesiomorphic species of catostomids are usually restricted to lowlands in basins (Figure 6), where they inhabit low-gradient rivers or lakes in a vicariant pattern. These species are *C. ardens* in the Bonneville Basin, *C. macrocheilus* in the Harney–Malheur Basin (and Columbia River basin), *C. warnerensis* in the Warner Lakes basin, *C. tahoensis* in the Lahontan Basin, *C. fumeiventris* in the Owens River basin, and *C. shoshonensis* in Wall Canyon of Surprise Valley (Appendix, numbers 66–75; Figures 5, 6). Fossil *Catostomus* (10 Ma to Holocene) are known from the north edge of the Great Basin, which is along the southern margin of the Snake River Plain.

The mountain suckers (*C. columbianus*, *C. platyrhynchus*, *C. discobolus*, *C. clarki*) are morphologically derived (Smith, 1992b). They inhabit high-gradient streams and stream headwaters, and they have been broadly dispersed by many headwater transfers (Figure 7; Smith, 1966). *Catostomus platyrhynchus* has been transferred from the Bonneville Basin to the Lahontan Basin and to the drainages of the Snake/Columbia, Colorado, and Missouri Rivers. *Catostomus discobolus* is native to the upper Colorado River, including the Grand Canyon, and has been transferred among the Colorado River and Snake River drainages to the Bear and Weber Rivers in the northern Bonneville Basin. *Catostomus clarki* is found in the drainages of the Gila, Virgin, and White Rivers, but not the Colorado River in and above the Grand Canyon, and it helps define the Pliocene drainage of the Bouse Embayment of the Gulf of California during the time when it might have been blocked from its connection with the upper Colorado River drainage (Taylor, 1983). *Catostomus santaanae*, in the Los Angeles area (Figure 7), is the sister species to the Colorado River species, *C. discobolus* and *C. clarki*. *Catostomus santaanae* represents the population that lived in the lowest Colorado Paleoriver when it flowed to its Los Angeles delta, prior to 9 Ma. *Catostomus columbianus* inhabits both the Harney–Malheur Basin and the Columbia River drainage and helps to define the overflow through the South Fork of the Malheur River to the Snake River across the Voltage lava flow (Piper et al., 1939), which occurred as recently as about 9000 years B.P. (Gehr and Newman, 1978).

ICTALURIDAE.—North American catfishes of the genus *Ameiurus* were rare in the Great Basin. Two Miocene forms are known (Appendix, numbers 80, 81), one from the Truckee Formation in Nevada and one from formations in the Salt Lake group in northern Utah. Their relatives include fossils in the Pliocene Columbia River, Miocene and Pliocene Snake River, and Miocene to Holocene rivers in eastern North America (Lundberg, 1992; Smith et al., 2000). These occurrences provide additional evidence for former Great Basin connections to the Snake River Plain and to south-central Washington before the formation of the modern Columbia drainage. The Miocene

form from northern Utah is most similar to bullheads of the Snake River Plain, supporting a Hemphillian or older connection between the Salt Lake group and Lake Idaho (Taylor, 1966; Stokes, 1979). No *Ameiurus* are known from the southwestern United States or Mexico, despite the diversity of other genera of catfishes in Mexico (Lundberg, 1992).

SALMONIDAE.—Eight native species of salmonids apparently inhabited the Great Basin in recent times: rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*, with many subspecies), bull trout (*Salvelinus confluentus*), four whitefishes (*Prosopium* spp.), and possibly the Arctic grayling (*Thymallus arcticus*). Additional trouts and char are represented in the fossil record. Salmonids are cool-water fishes that inhabit mountain streams and deep lakes. Their distribution patterns indicate that they dispersed among basins via headwater-stream captures as well as by discharge from pluvial lakes. During interglacial times (such as the present), desiccation and warming of aquatic habitats restricts these fishes to small populations in a few cool lakes, rivers, and headwaters. During pluvial stages of the last 3 My, however, there were numerous, large populations (see Appendix) in large, deep lakes and large rivers. Salmonids from the Miocene, Pliocene, and Pleistocene are known to have occurred in lake basins, such as the Salt Lake group, Fort Rock Lake basin, Lahontan Basin, Honey Lake basin, Bonneville Basin, and Owens Basin. Holocene salmonids are found in drainages west, north, and east of the Great Basin, and in a few drainages at high elevations in Mexico.

COREGONINAE. There are six recent species of whitefishes in the genus *Prosopium* of the subfamily Coregoninae. Four live in the Great Basin; three of these are endemic to Bear Lake in Utah and Idaho (Appendix, numbers 82–85). The other two, *P. cylindraceum* and *P. coulteri*, inhabit eastern to northwestern North America and Siberia (Smith and Todd, 1993). At least one fossil species, *P. proluxus* Smith (1975), is common in Pliocene sediments of the Snake River Plain. The morphologically based, cladistic estimate of relationships of the species in the group is shown on a distribution map (Figure 8). Unpublished molecular data (Shiozawa) indicates a more complicated pattern than that depicted in Figure 8. *Prosopium* illustrates intralacustrine as well as allopatric speciation in Bear Lake and in subbasins of the Bonneville–Bear system. As predicted by the intralacustrine speciation hypothesis, the differentiated characters among the species of *Prosopium* are mostly associated with feeding: the shape of the mouth and jaw and the numbers of teeth, gill-rakers, and pyloric caeca (Smith and Todd, 1993). The phylogenetic pattern indicates that the most-derived forms in the genus evolved in the Bonneville Basin and Bear Lake.

THYMALLINAE. Grayling (*Thymallus*) have not been regarded as part of the Great Basin fauna. There are no fossil or Holocene specimens documenting their presence. Inclusion in the present list is based upon the apparently knowledgeable identifications in the journal of John Townsend (1978), who recorded collecting grayling in the Bear River in 1834 (Appendix, number 86).

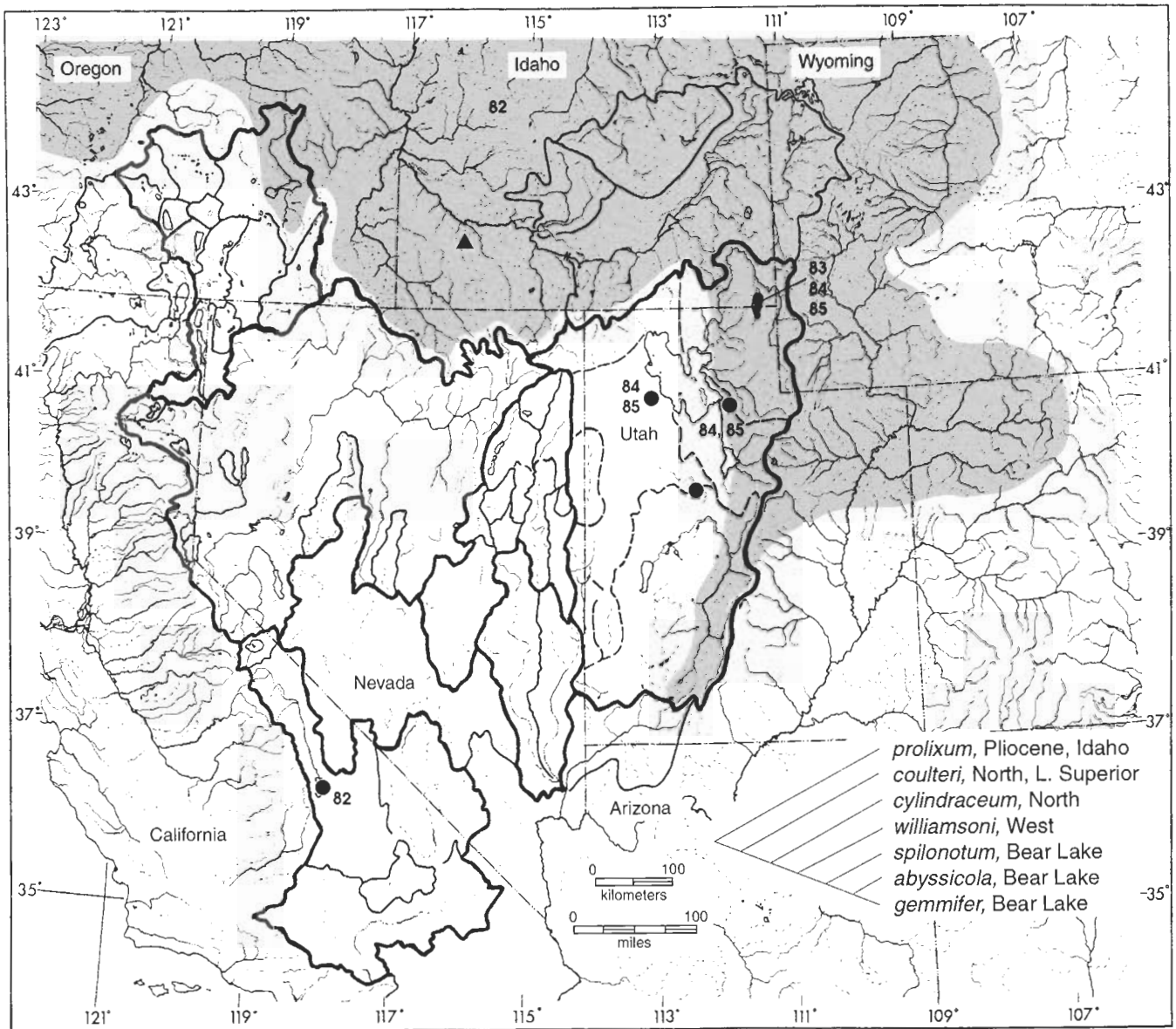


FIGURE 8.—Native distribution of *Prosopium* (shown with shading) in the Great Basin and nearby drainages, with estimate of the phylogenetic tree (from Smith and Todd, 1993). Shading indicates drainage basins occupied by species (as numbered in the Appendix). Symbols representing fossil ages are defined in Figure 1.

SALMONINAE: Settlers in the nineteenth century found abundant trout in many northern Great Basin lakes and streams (map, Figure 9), but these were quickly overexploited (Behnke, 1992). By the 1930s, introduced hatchery fish began to cloud the possibilities for interpreting salmonid and hydrographic history (Behnke, 1981, 1992), and unfortunately museum specimens that predate these introductions are sparse. Modern protein and mtDNA studies are, however, discriminating native from introduced stocks and are adding considerable historic information (Leary et al., 1984, 1987). Trout are adapted to cold lakes and streams and to high gradients. Stream forms survived arid times at high elevations and gla-

cial times in large lakes. There are indications that, in addition to trouts (*Oncorhynchus*), at least two char (*Salvelinus*) were native to the northern Great Basin; this evidence is reviewed in the Appendix (number 87). The fossil record of *Salvelinus* is older than the fossil record of *Oncorhynchus*. *Salvelinus* was in the Great Basin (central Nevada) and northern Idaho in the middle Miocene and in the Snake River Plain in the late Miocene.

The late Miocene *Oncorhynchus* of the Truckee Formation differs in many characters from modern species of *Oncorhynchus*. It possesses synapomorphies that are shared by *O. clarki*, indicating it is more advanced than the basal Mexican golden

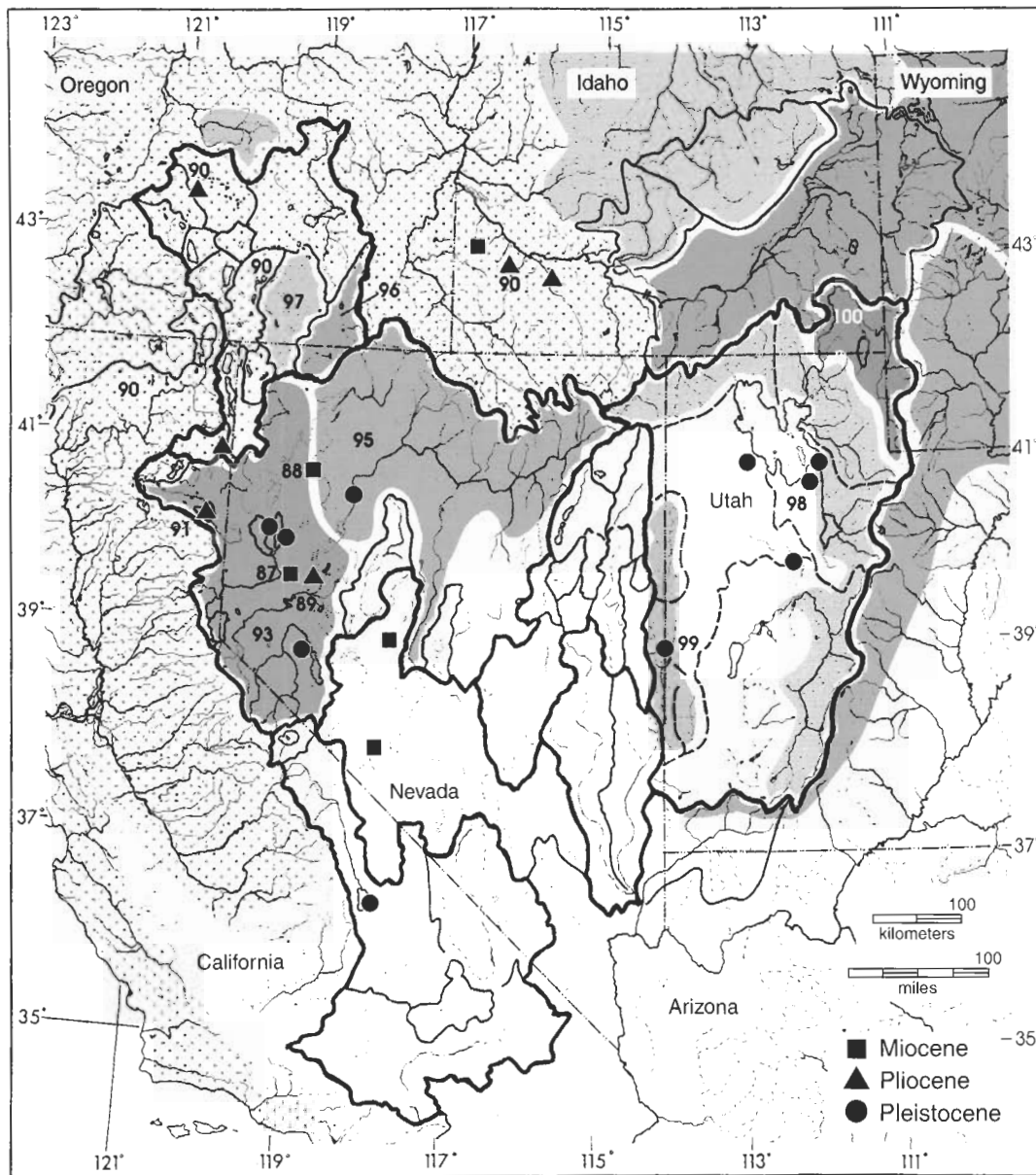


FIGURE 9.—Distribution of Holocene and fossil species and subspecies of rainbow trout (*Oncorhynchus mykiss*, stipple pattern) and cutthroat trout (*O. clarki*, shaded patterns) in the Great Basin and adjacent drainages. Shading indicates drainage basins occupied by species and subspecies (as numbered in the Appendix). Squares = Miocene; triangles = Pliocene; bullets = Pleistocene.

trout, *O. chrysogaster*. The characteristics of the Truckee trout indicate that it existed before the differentiation of rainbow trout and cutthroat trout (Stearley and Smith, 1993), while its habitat was connected to the Pacific Ocean. As early as late Miocene and throughout the Pliocene, the trout, †*Oncorhynchus* (“*Rhabdofario*”) *lacustris* (Cope), of the lower Snake River drainage and northwestern Nevada, shows a composite of *O. clarki* (cutthroat trout) and *O. mykiss* (rainbow trout) characters, e.g., *O. clarki* dentaries, intermediate maxillae, and *O. mykiss* premaxillae. These characters diagnose either the ancestor prior to the *clarki*–*mykiss* divergence or the ancestral

redband trout (*Oncorhynchus mykiss gairdneri*). The distinction cannot be made at this time because intermediates between *O. clarki* and *O. mykiss* still exist, especially in the Columbia Basin. Characters of these trout subsequently sorted into *O. mykiss* and *O. clarki* elsewhere, but they continue to be introgressed or unsorted in redband trout throughout their range in the lower Columbia River, Klamath River, and Sacramento River drainages (Leary et al., 1984, 1987; Berg, 1987; Allendorf and Leary, 1988), possibly throughout much of the last 3 My. A sample of hatchery-produced *O. mykiss* differs from *O. clarki* by 3.7% mtDNA (Table 3).

TABLE 3.—Sequence divergences, based on mtDNA restriction-site data, for *Oncorhynchus clarki* populations and their outgroup species, *Oncorhynchus mykiss*. (Cr. = Creek, R. = River.)

Species or population	<i>O. mykiss</i>	Trout	Deaf Smith	Sevier	Bear	Yellow-stone	Snake	Sedge	Current	Sheep	Mack	Flynn	Fish	Wing	Cougar	Wash-burn	Humbolt	Silver-king	Willow	White-horse
<i>O. mykiss</i>	0																			
Trout Cr.	0.039	0																		
Deaf Smith Cr.	0.057	0.023	0																	
Sevier R.	0.036	0.008	0.023	0																
Bear R.	0.041	0.014	0.035	0.015	0															
Yellowstone R.	0.036	0.014	0.035	0.015	0.004	0														
Snake R.	0.037	0.012	0.035	0.013	0.003	0.002	0													
Sedge Cr.	0.037	0.012	0.035	0.013	0.003	0.002	0.007	0												
Current Cr.	0.033	0.012	0.032	0.010	0.009	0.008	0.007	0.007	0											
Sheep Cr.	0.033	0.012	0.032	0.009	0.009	0.008	0.007	0.007	0	0										
Mack Cr.	0.040	0.018	0.040	0.017	0.018	0.018	0.018	0.018	0.014	0.014	0									
Flynn Cr.	0.040	0.018	0.040	0.017	0.018	0.018	0.018	0.018	0.014	0.014	0	0								
Fish Cr.	0.037	0.018	0.040	0.016	0.016	0.016	0.016	0.016	0.016	0.010	0.011	0.011	0							
Wing Cr.	0.036	0.019	0.040	0.016	0.014	0.014	0.014	0.014	0.009	0.009	0.014	0.014	0.003	0						
Cougar Cr.	0.037	0.020	0.042	0.017	0.013	0.013	0.012	0.012	0.009	0.009	0.014	0.014	0.004	0.001	0					
Washburn Cr.	0.042	0.022	0.036	0.020	0.018	0.018	0.018	0.018	0.012	0.012	0.018	0.018	0.009	0.007	0.008	0				
Humbolt R.	0.042	0.022	0.036	0.020	0.018	0.018	0.018	0.018	0.012	0.012	0.018	0.018	0.009	0.007	0.008	0.001	0			
Silverking Cr.	0.042	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.017	0.017	0.009	0.007	0.008	0.001	0.001	0		
Willow Cr.	0.041	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.016	0.016	0.009	0.007	0.008	0.001	0.001	0.001	0	
Whitehorse Cr.	0.041	0.023	0.035	0.019	0.017	0.017	0.017	0.017	0.011	0.011	0.016	0.016	0.009	0.007	0.008	0.001	0.001	0.001	0	0

Oncorhynchus clarki, the cutthroat trout, has been in the Great Basin longer than proposed by Behnke (1981, 1992), according to the Miocene fossil record. Molecular data indicate that interbasin differentiation of *O. clarki* subspecies goes back nearly 5 My, into the Pliocene (Table 3).

The Great Basin trouts form three clades. The Bonneville Basin clade is cladistically basal, being the sister group to the remainder of the species (Figure 10). The Snake River clade is the next-most basal group, and it includes the Bear River form. Although the Bear River is now a tributary to the northern Bonneville Basin, it was part of the Snake River drainage prior to 20–15 Ka (McCoy, 1987; Curry, 1990; Bouchard et al., 1998). The Lahontan Basin and southern Oregon subspecies are a sister group to the westslope trout subspecies, *O. c. lewisi*. Coastal cutthroat trouts, *O. c. clarki*, are an intermediate clade between the Colorado River plus Snake River groups and the Westslope plus Oregon–Lahontan groups (Figures 9, 10).

Fort Rock Valley, west of the Harney–Malheur Basin in Lake County, Oregon, was the site of Fort Rock Lake, also called Fossil Lake, which was a tributary to the Deschutes and Columbia Rivers prior to blockage of the outlet by postglacial lava flows (Allison, 1940, 1982). Pliocene and Pleistocene sediments in the Fort Rock Valley contain trouts, minnows, and suckers. A Pliocene salmon from diatomaceous sediments of the Fort Rock Formation, *Oncorhynchus* sp. (either *nerka*, *keta*, or *gorbuscha*), was reported by Cavender and Miller (1972). The trout specimens in this basin (*Oncorhynchus* sp.; Appendix, number 90) are osteologically similar to redband trout and were considered to date from the late Pleistocene by Allison and Bond (1983). They based their conclusion upon shared characters of the palatine, maxilla, hyomandibular, and orbitosphenoid. More than 50 dentaries from Fossil Lake were examined for the present study. Forty-seven maxillae have a mixture of modern *O. clarki* (from Pyramid Lake before introductions) features and features of Pliocene *O. lacustris* (pre-*clarki* and pre-*mykiss*) of the Snake River Plain, whereas seven maxillae resemble *O. m. gairdneri* (redband trout). One premaxilla resembles that of *O. clarki* and seven resemble that of *O. mykiss*, but it is not clear whether the differences represent variability in one species. Palatines from Fossil Lake are deep, like that of *O. lacustris*, and the hyomandibular is angled posteroventrally, also like that of *O. lacustris*.

The Pliocene fish fauna of Secret Valley, Modoc County, California (*Oncorhynchus* (Appendix, number 91), *Klamathella*, *Ptychocheilus*, *Lavinia*, *Chasmistes*, and possibly *Acrocheilus* and *Cottus*), and the Pliocene fish fauna of the Snake River Plain are very similar; this suggests the two drainages were connected prior to the Pliocene (Wheeler and Cook, 1954; Miller and Smith, 1981; Wagner et al., 1997). A similar fauna from the nearby Alturas Basin, Modoc County, California, contains *Klamathella*, *Ptychocheilus*, *Chasmistes*, and *Catostomus* (Wagner et al., 1997). These similarities suggest former hydrographic connections (not necessarily contemporaneous) among the Pit River, the Snake River, and the Klamath Basin.

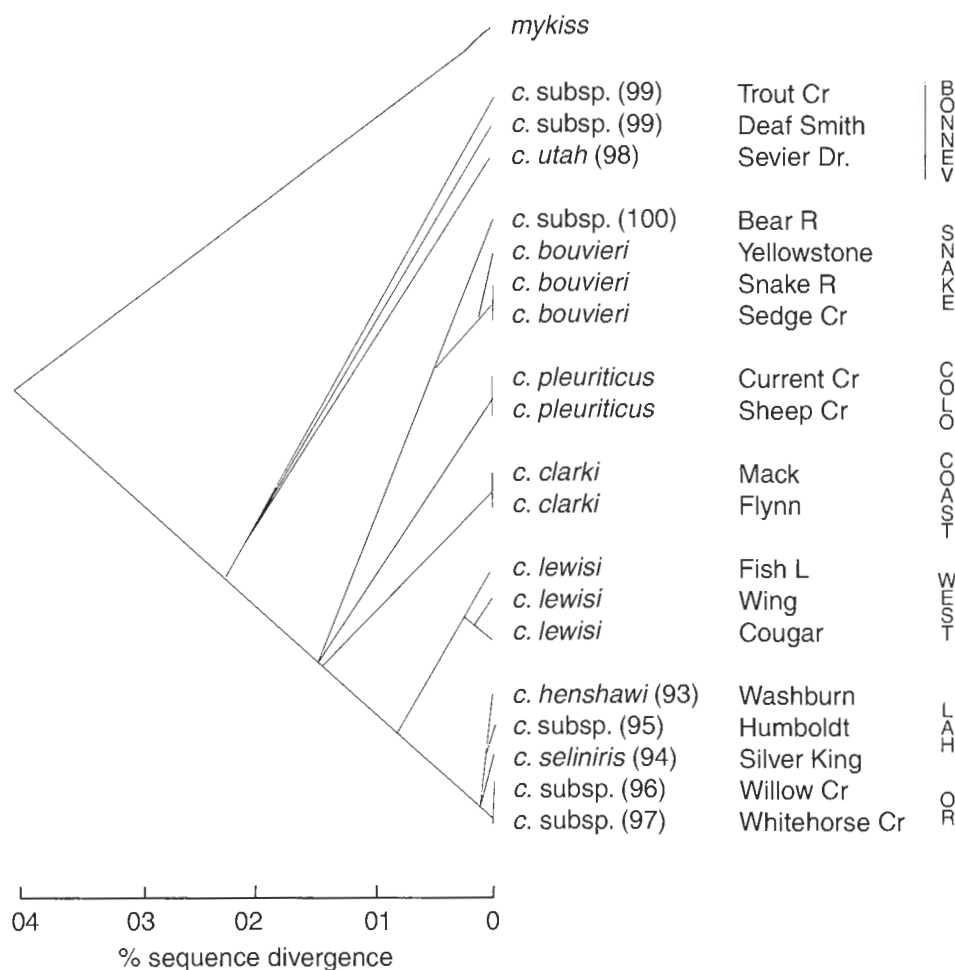


FIGURE 10.—Estimate of the phylogenetic tree of *Oncorhynchus clarki* (cutthroat trout) and its outgroup, *Oncorhynchus mykiss*, based on restriction fragment analysis of mtDNA. Branch lengths may be read as estimated time if divided by the calculated rate of 0.5% sequence divergence per 1 My. Abbreviations: BONNEVE = Bonneville Basin, SNAKE = Snake River drainage, COLO = Colorado River drainage, COAST = Coastal drainages, WEST = west slope drainages, LAH = Lahontan Basin, OR = Oregon Lakes drainages, southeast Oregon.

CYPRINODONTIDAE.—The Great Basin pupfishes are the showpiece of Great Basin ichthyology. They were the focus of R.R. Miller's doctoral research, the results of which were published in his 1948 monograph. This monumental systematic and experimental work illustrated the relationship between isolation and differentiation in relict waters. Pupfishes of the Great Basin's Death Valley system (Miller, 1946a) have been the subject of extensive ecological and physiological studies (Brown and Feldmeth, 1971; Soltz and Naiman, 1978; Feldmeth, 1981), behavioral observations (Liu in Turner, 1974), biochemical comparisons (Turner, 1984; Echelle and Echelle, 1993), and molecular analyses (Echelle and Dowling, 1992; Parker and Kornfield, 1995). Relationships of these species are now understood to be more complex than formerly thought. *Cyprinodon radiosus* (Appendix, number 101) of the Owens River is the sister species to *C. macularius* of the lower

Colorado River, and these two species are the sister group to the clade that includes *C. salinus*, *C. nevadensis*, *C. diabolis*, and relatives, in the Salt River, the Amargosa River, Devil's Hole, and Ash Meadows (Figure 11; Appendix, numbers 102–110). This Death Valley and Ash Meadows clade possibly includes *Cyprinodon fontinalis* of northern Chihuahua, Mexico (Figure 11), but this is not consistent with geography or scale morphology (Miller and Smith, 1986; Minckley et al., 1986). Hydrographic connections among basins and with drainages in Mexico are indicated by *Cyprinodon* mtDNA analysis (Figure 11; Table 4; Echelle and Dowling, 1992; Echelle and Echelle, 1993) and molluscan data (Hershler and Pratt, 1990). Study of the data usually regarded as indicative of the relationship between isolation and divergence reveals interesting conflicts—molecular, biochemical, and morphological divergence and reproductive isolation are incongruent

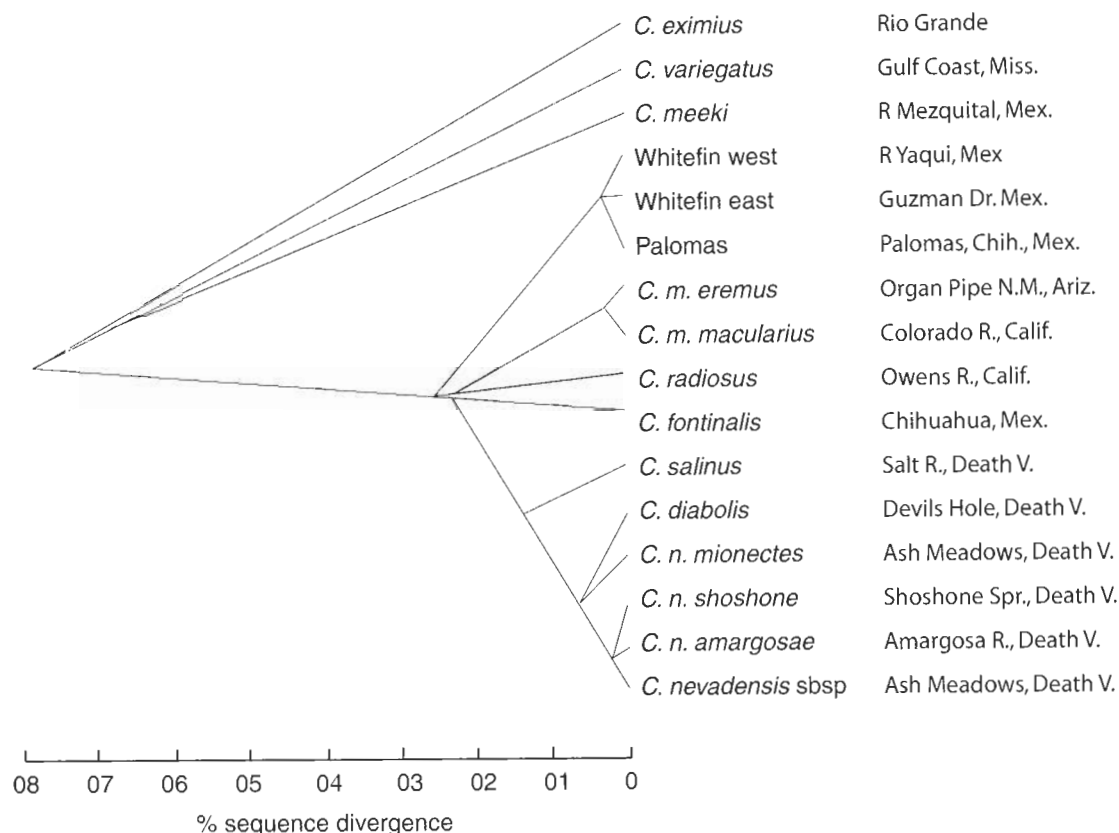


FIGURE 11.—Phylogenetic relationships (strict consensus tree) of certain western North American *Cyprinodon*, based upon parsimony analysis of mtDNA restriction site data (Data and trees from Echelle and Dowling, 1992). The Death Valley species are *C. C. nevadensis*, *C. salinus*, and *C. diabolis*; *C. milleri* has *C. salinus* mtDNA. *Cyprinodon radiosus* is the Owens River species, and *C. macularius* is in the lower Colorado River and vicinity. The other species are primarily from Mexico (Echelle and Dowling, 1992). The depth to each node may be scaled to age in millions of years, assuming that 1 My corresponds to 1% of the average percent sequence divergence between clades.

with each other and with evidence for timing of divergence (Turner, 1974; Echelle and Dowling, 1992; Echelle and Echelle, 1993). Cladistically analysed molecular data indicate that *Cyprinodon* has been in the Death Valley system for about 3 My. Biogeographic relationships of *Cyprinodon* (and good-eids) of the Great Basin are to the south, in Mexico, especially if *C. fontinalis*, from Chihuahua, is related to the Death Valley clade (Figure 11). The diversity of *Cyprinodon* species within the Great Basin, taken with its sister species, *C. macularius* Baird and Girard, displays a geographic pattern that extends from Death Valley and the Owens River to across the Gila River and the lower Colorado River drainages (Minckley et al., 1986).

Pliocene connections from the lower Colorado River to the Owens, Mohave, and Amargosa Rivers occurred about 3 Ma, according to molecular data (Figure 11; Table 4). The connections possibly involved China Lake, Searles Lake, Panamint Valley, and Wingate Pass to Lake Manly, now Death Valley, according to fish and other evidence (Miller, 1946a; Hubbs and Miller, 1948a; Benson et al., 1990). The Pliocene Owens–Mo-

have drainage connected to the lower Colorado River drainage (Blackwelder, 1933, 1954; Hale, 1985) near the region of Ludlow Pass (at 594 m), Bristol Lake, and Cadiz Lake. Brown and Rosen (1995) found no evidence of a through-flowing connection across the present topography, and they suggested alternative dispersal processes, routes, or times; however, rounded boulders in a large paleochannel, which are evidence of a through-flowing stream, are present near Ludlow (Hale, 1985; G.I. Smith, pers. comm. to G.R.S., 1999). Encroachment of the Gulf of California toward Death Valley (Durham and Allison, 1960) and the presence of foraminifera correlated with the Bouse Formation in cores taken from the dry lakes of Danby and Cadiz in southeastern San Bernardino County, California (P.B. Smith, 1960, 1970), suggest a connection existed to the estuary of the lower Colorado River. The most compelling fish evidence for a connection between the Mohave and Colorado Rivers is the distribution of *Cyprinodon macularius* of the lower Colorado drainage and *C. radiosus* of the Owens River. Mitochondrial DNA of these two species indicates they had a common ancestry between 2 and 3 Ma (Table 4).

TABLE 4.—Sequence divergences, based on mtDNA restriction-site data, for selected western North American *Cyprinodon* (Figure 11). See text for localities.

Species or subspecies	<i>C. eximius</i>	<i>C. variegatus</i>	<i>C. meeki</i>	Whitefin pupfish(w)	Whitefin pupfish(e)	Palomas pupfish	<i>C. m. eremus</i>	<i>C. m. macularius</i>	<i>C. r. radiosus</i>	<i>C. fontinalis</i>	<i>C. salinus</i>	<i>C. diabolis</i>	<i>C. n. mionectes</i>	<i>C. n. shoshone</i>	<i>C. n. amargosae</i>
<i>C. eximius</i>	0														
<i>C. variegatus</i>	0.083	0													
<i>C. meeki</i>	0.073	0.068	0												
Whitefin pupfish (west)	0.060	0.068	0.069	0											
Whitefin pupfish (east)	0.056	0.068	0.069	0.006											
Palomas pupfish	0.059	0.066	0.068	0.002	0										
<i>C. m. eremus</i>	0.074	0.073	0.069	0.019	0.022	0	0								
<i>C. m. macularius</i>	0.076	0.075	0.071	0.019	0.023	0.021	0.003	0							
<i>C. radiosus</i>	0.077	0.095	0.082	0.028	0.028	0.027	0.027	0.028	0						
<i>C. fontinalis</i>	0.063	0.061	0.068	0.015	0.033	0.032	0.036	0.033	0.035	0					
<i>C. salinus</i>	0.082	0.082	0.087	0.033	0.028	0.026	0.031	0.036	0.037	0.019	0.012	0			
<i>C. diabolis</i>	0.075	0.075	0.080	0.028	0.029	0.027	0.032	0.036	0.038	0.020	0.013	0.005	0		
<i>C. n. mionectes</i>	0.075	0.080	0.075	0.029	0.022	0.020	0.028	0.033	0.035	0.028	0.013	0.005	0.006	0	
<i>C. n. shoshone</i>	0.072	0.082	0.077	0.022	0.026	0.024	0.032	0.037	0.035	0.024	0.013	0.005	0.006	0.003	0
<i>C. n. amargosae</i> (Tecopa)	0.077	0.077	0.077	0.026	0.024	0.022	0.030	0.035	0.032	0.022	0.012	0.003	0.005	0.002	0.002
<i>C. nevadensis</i> subsp.	0.074	0.078	0.078	0.024	0.024	0.022	0.030	0.035	0.032	0.022	0.012	0.003	0.005	0.002	0.002

GOODEIDAE.—The poolfishes and springfishes, *Empetrichthys* and *Crenichthys*, respectively (Appendix, numbers 112–115), are Great Basin endemics in the subfamily Empetrichthyinae (Webb, 1998) of the family Goodeidae (Parenti, 1981; Grant and Riddle, 1995). *Empetrichthys* and *Crenichthys* are oviparous and were formerly classified as cyprinodontids, but Parenti's (1981) phylogenetic evidence demonstrated their relationship to the live-bearing goodeids of the Mexican Plateau. Empetrichthyines resemble fundulids in osteology, numbers of fin rays, and tooth form, which distinguish them from the cyprinodontids, but unlike fundulids, they lack pelvic fins. Fossil *Empetrichthys* were discovered from the Pliocene near Los Angeles, California, and from the Pleistocene in southern Nevada (see Appendix, number 112). Paleontological studies by M.L. Smith (in Miller and Smith, 1986) and molecular studies by Webb (1998) indicate middle to late Miocene goodeid vicariance between the White River and the lower Colorado River drainages and the Mexican Plateau, probably involving tributaries of the Bouse Embayment and the Gulf of California. The distribution of fossil and Holocene *Empetrichthys*, *Fundulus*, and *Gasterosteus*, along with species of *Pyrgulopsis* (hydrobiid snails), provide evidence that late Miocene lowland Pacific coast tributaries flowed westward from west-central Nevada and Death Valley across a lower, proto-Sierra Nevada (Bell, 1979; Hershler and Pratt, 1990) about 6 Ma, perhaps through the (reversed) Mohave River valley (Weldon, 1982).

FUNDULIDAE.—Most species of killifish in the family Fundulidae live in eastern North America, but there are representatives in Mexico and California. Several fossil forms were described (Miller, 1945b) before it was recognized (Parenti, 1981) that the Goodeidae of the Mexican Plateau, relatives of Fundulidae, are represented in the Great Basin. The Nevada fossils (Appendix, numbers 116–123) have some observable characters that suggest they could be related to the Empetrichthyinae or the Goodeidae (Miller, 1948:100), except that none of the Nevada fossils lack pelvic fins, as do the empetrichthyines.

The ancient diversity of fundulids in the southwestern Great Basin is remarkable, considering the paucity of other genera (except *Siphateles* and *Gasterosteus*) in the fossil record from there (M.L. Smith, 1981) and the absence of *Fundulus* in the Great Basin today. The presence of fundulids from northeast (Humboldt Formation) and west-central (Truckee Formation) Nevada and Death Valley through most of the Miocene and Pliocene establishes a benchmark of antiquity that is important, given that the ages of origin of Great Basin fish groups are underestimated (see "Material and Methods" and the Appendix).

COTTIDAE.—The Cottidae, like the Salmonidae, are low-temperature, usually high-gradient fishes. They occupy mountain streams and cold lakes. Their fossil record in the Great Basin goes back to the Pliocene and Pleistocene in the Lahontan Basin (*C. beldingi*) and to the late Pleistocene in the Bonneville Basin (*C. bairdi*, *C. extensus*). Their phylogenetic relationships are to the north and west. More species of northwestern

sculpins occur in the northern Bonneville Basin and Bear River drainages than are currently acknowledged in the literature, according to new discoveries by Shiozawa and others (unpublished). Sculpins are not found with cyprinodontoids in western North America, unlike their occasional sympatry in the eastern United States, reflecting the more extreme habitat gradients (temperature and stream profiles) in the west.

GASTEROSTEIDAE.—The Miocene three-spined stickleback (*Gasterosteus doryssus*; Appendix, number 128) occurs in the Great Basin from the Truckee Formation in west-central Nevada from Hazen (Bell, 1974) to the Sahwave Mountains (LaRivers, 1964). It represents a fauna that colonized the basin prior to final elimination of the drainage outlet to the Pacific coast by the Sierra Nevada uplift (Bell et al., 1985). The Nevada *Gasterosteus* is the most significant fossil fish lineage in the Great Basin, if not in Cenozoic ichthyology in general, because of the abundant, beautifully preserved samples in annual laminae of diatomite and the detailed studies of these samples by Bell and his students (Bell and Haglund, 1982; Bell, 1994, and references therein). In brief, the study of more than 8000 specimens from a 110,000-year time sequence has shown rapidly fluctuating but gradual change, with no stasis (Figure 12). Bell (1994) concluded that much of the change can be attributed to selection, but some seems uncorrelated with environmental change.

Gasterosteus aculeatus aculeatus (Appendix, number 129), the modern, anadromous, fully plated, three-spined relative, was reported from the late Miocene Monterey Formation at Lompoc, California, by Bell (1977), strengthening the hypothesis that inland freshwater populations of sticklebacks were independently derived from a widespread anadromous form (Bell, 1979). Comparison of these sticklebacks demonstrates that new species can arise repeatedly, as restricted peripatric and paraphyletic derivative populations, without effects on the ecology, morphology, or long-term history of the widespread, ancestral species. Bell's point demonstrates the logical difficulties attending Hennig's rule (1966), which requires changing a

species name with each branching event in a clade's history, if the parent species did not change while daughter lineages were produced (Bell, 1979).

CENTRARCHIDAE.—Sunfish occupied lakes and streams in western North America from Idaho, Washington, and Oregon to Nevada and northern Utah (Salt Lake group) during the Miocene and Pliocene. The Nevada specimens suggest that the climate during the middle to late Miocene was warm and that the basin floor was at low elevations, but floristic data indicate the floor was at higher elevations (Wolfe et al., 1997). The combination suggests local topographic extremes. There was more diversity during the Miocene than is recognized in the currently defined genera *Archoplites* and *Plioplarchus*. An undescribed form existed in the Miocene of Oregon (Appendix, number 130). Modern centrarchids are restricted to *Archoplites* of the Great Valley, California, and to a radiation of nine genera and more than 30 species in the Atlantic coastal drainages of North America.

Discussion

FISH BIOGEOGRAPHY AND GEOLOGICAL TIME

RELATIONSHIP BETWEEN PHYSIOGRAPHIC AND BIOLOGICAL EVIDENCE.—Hubbs and Miller's search for congruence between physiographic and ichthyological histories is evident throughout their 1948b monograph. They noted, for example, the local morphological distinctiveness of *Siphateles*, *Rhinichthys*, and *Cyprinodon* as evidence of postpluvial separation of previously uniform gene pools (Hubbs and Miller, 1948b:66, 83, 91). The seemingly parsimonious assumption that faunas were uniform at the time of the last habitat connection has rarely been questioned (Kocher and Stepien, 1997), but even in 1948, it was in conflict with the fossil record of modern fishes, which, when known, extended back beyond Pleistocene events to the Pliocene or Miocene (Hubbs and Miller, 1948b:25–27).

Taylor (1960) noted the antiquity of many modern lineages of mollusks and fishes and suggested that they are much older than modern physiography, ice ages, and pluvials. The corollary of this suggestion is that the tectonic, volcanic, and glacial changes in the landscape occur more rapidly than the evolving changes in lineages on that landscape. Taylor's principle suggests that we cannot assume that the observed amount of species and subspecies evolution automatically occurred in the interval since the most recent possible geological changes and vicariance events. Multiple possible vicariant times should be among the tested alternatives. For example, the assumption that cladogenesis of Holocene birds originated in the Pleistocene was refuted by Klicka and Zink (1997), who demonstrated that numerous supposedly Pleistocene species date back to the Pliocene. Our interpretations of fossil fish specimens combined with DNA analyses and phylogenetic analyses of Holocene species indicate that the ages of clades and vicariance barriers have usually been underestimated, thereby challenging the frequent assumption that the most recent possible connection was the operative one.

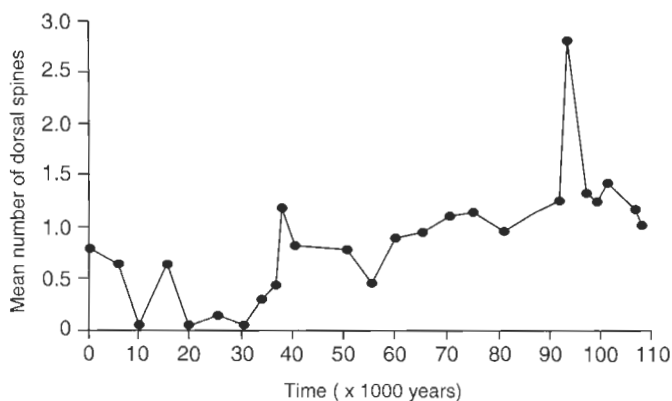


FIGURE 12.—Variation in mean number of dorsal spines in *Gasterosteus doryssus*. Variation shows rapid short-term changes and slow long-term trend (after Bell et al., 1985).

Phylogenetic estimates for the Cyprinidae (Figures 2, 3), Catostomidae (Figure 5), Coregoninae (Figure 8), *Oncorhynchus* (Figure 10), and Cyprinodontidae (Figure 11) are presented in the figures with key words for taxon geography to provide background for examining the relative timing of historic hydrographic connections among basins. Traditional studies (Hubbs and Miller, 1948b; Smith, 1966, 1978; Hubbs et al., 1974; Minckley et al., 1986) and the new phylogenies enable the formulation of hypotheses concerning the relative ages of barriers.

According to the phylogenies, moderately old and prominent barriers separated the Great Basin from its neighboring drainages to the east and the Sacramento Basin to the west. Phylogenetic indicators of the barrier between the Great Basin and the Colorado Basin, for example, are the relative antiquity of the nodes between the *Gila atraria* group and the *G. robusta* group (Figures 2, 3), between *Xyrauchen* and *Chasmistes*, between *Catostomus ardens* and *C. latipinnis*, between *C. platyrhynchus* and *C. discobolus* (Figure 5), and between *Oncorhynchus clarki utah* and *O. c. pleuriticus* (Figures 9, 10). The importance of the Sierra Nevada as a barrier is indicated by the separation of *Catostomus occidentalis* and *C. microps* from *C. tahoensis* (Figure 5), and by *Oncorhynchus mykiss* from *O. clarki* (Figures 9, 10). A strong barrier separated the Bonneville and Lahontan Basins along the original line of separation in the Great Basin, as illustrated by the relative distance between nodes, for example, between nodes for *Gila* and *Siphateles* (Figures 2, 3), *C. ardens* and *C. tahoensis* (Figure 5), and *O. c. utah* and *O. c. henshawi* (Figures 9, 10). The moderately strong separation of the Lahontan Basin and Colorado Basin drainages is illustrated by the nodal distances between *Gila* and *Siphateles* (Figures 2, 3), *C. tahoensis* and *C. latipinnis* (Figure 5), and *O. c. henshawi* and *O. c. pleuriticus* (Figures 9, 10). The weakest, most recent barriers separated the Lahontan Basin and Death Valley systems, and the subdrainages within the Bonneville, Lahontan, White River, and Death Valley systems (most examples are similar species or subspecies not shown on the phylogenies), but all of these barriers have been breached by headwater-stream captures, indicated by some of the examples below and in Figures 2, 3, 5, and especially Figure 10.

Fish distributions suggest that much of the drainage from the area of the Great Basin flowed to the Pacific Ocean at times during the Miocene, Pliocene, and Pleistocene, even though the Basin and Range topography began forming more than 15 Ma. The fish data presented herein indicate that these hydrologic confluences probably had an episodic history that began much earlier than the most recent known connection.

MIocene.—Geological and paleontological studies indicate that at times during the Miocene, the Death Valley, Lahontan, and Bonneville systems drained westward to the Pacific Ocean (Bell, 1974, 1994; Stokes, 1979; Taylor, 1985; Minckley et al., 1986; G.I. Smith, pers. comm. to G.R.S., 1999). Some Miocene biogeographic patterns, however, were dominated by north–south systems (Taylor, 1985) that were congruent with

the north–south structures that resulted from convergence of the west coast of North America with the Pacific Plate (Figure 13). Early hydrographic connections occurred between the Humboldt lacustrine system and the western Snake River Plain and southeastern Oregon, according to Stokes (1979) and evidence from the distribution of Centrarchidae. Later in the Hemphillian, the Salt Lake group, with a relatively rich fish fauna in the northern Bonneville Basin, was probably connected to the eastern Snake River Plain (McClellan, 1977). The fish fauna was related to, but specifically different from, that of the western Snake River Plain (McClellan and G.R. Smith, In press). The presence of *Lavinia* in the lower Salt Lake group indicates there were earlier connections to the western Snake River Plain and the Pacific coastal drainages. *Lavinia* is now restricted to the Sacramento drainage. The mixture of lowland fish faunas and upland floras in Nevada during the Miocene (Wolfe et al., 1997) suggests that evolution of regional topographic relief took place subsequently (Orr, 1982; Pierce and Morgan, 1992).

LATE MIOCENE TO PLIOCENE.—The southern Lahontan Basin fossils from the late Miocene and Pliocene are indicative of low elevations, but the northern Lahontan Basin fossils are indicative of higher elevations. Elevations of the Snake River Plain were low in the late Miocene, but uplift of the eastern Snake River Plain at this time occurred in the path of the Yellowstone hot spot (Pierce and Morgan, 1992).

A connection from the Mono Lake area of the Great Basin to the San Joaquin River ended when basalt dammed the V-shaped channel near Deadman Pass in the Devil's Postpile quadrangle (Huber and Rinehart, 1965, 1967), causing cessation of river flow 3.2 Ma (Dalrymple, 1964; Huber, 1981). The channel is now at about 8400 ft (2580 m) elevation, having been raised 3120 ft (950 m) by uplift of the Sierra Nevada (Dalrymple, 1964; Huber, 1981), so the estimated elevation of the active channel was 5280 ft (1620 m; G.I. Smith et al., 1983; G.I. Smith, pers. comm. to G.R.S., 1999). The outlet possibly continued from the Great Valley across the Diablo Uplift to deposit the Monterey Fan (Cole and Armentrout, 1979). Cyprinid and gasterosteid fish connections require lower elevations during the late Miocene, based upon their present elevational restrictions.

PLIOCENE.—Our phylogenetic data suggest the occurrence of some ancient drainage connections that had not been previously noted (Figure 13). For example, the similarity of morphology and DNA (see below) of *Lepidomeda* from the Virgin River drainage and *Snyderichthys* from the upper Snake River and the Bear River drainages suggests there were connections from the upper Snake River to the Virgin River–White River drainage (Dowling et al., 2002). Keyes (1917), in a discussion of the origins of Lake Bonneville, proposed that the headwaters of the Snake River were formerly a tributary to the Virgin River. Ives (1948) presented evidence that Lake Bonneville drained from its Escalante arm to Meadow Valley Wash (a tributary to the Virgin River) prior to its drainage through Red

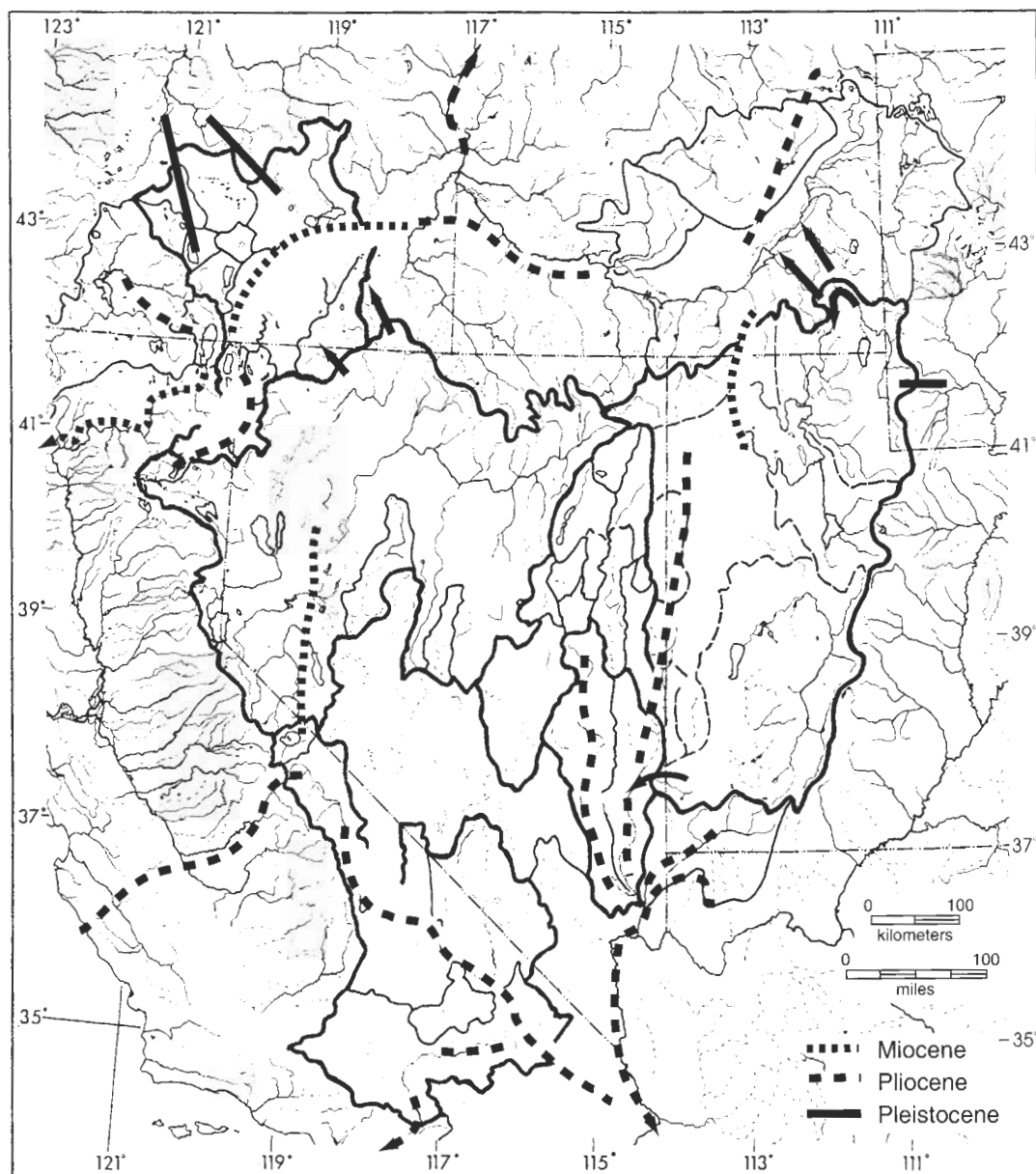


FIGURE 13.—Paleogeographic map showing major Miocene, Pliocene, and Pleistocene hydrographic connections, based upon our current interpretations of age and location and supplemented by the conclusions of Cole and Armentrout (1979), Taylor (1985), Taylor and Bright (1987), Ives (1948), and G.I. Smith (pers. comm. to G.R.S., 1999). Heavy dashed lines and arrows represent captures, overflows, or rivers. See "Discussion" and Appendix for the estimated timing of some of the barriers represented by lightweight lines.

Rock Pass to the upper Snake River. Hubbs and Miller (1948b) rejected these hypotheses as unsupported by fish evidence. Possible connections require serious consideration now because of new cyprinid and molluscan evidence. Miocene and Pliocene distributions of freshwater snails, namely, *Valvata idahoensis* Taylor, *Lutalimnea dineana* (Taylor), *L. gentilis* Taylor, and *Tryonia protea* (Gould), led Taylor (1985:285, 296, 317) to propose late Miocene and possibly Pliocene connections (not necessarily contemporaneous) from the upper Snake

River, through the Bonneville area, to the lower Colorado River drainage.

The White River canyon in southern Nevada is surrounded by possible drainage connections, as indicated generally by Taylor (1985, figs. 15, 25), leading to the Bouse Embayment of the Gulf of California in the late Miocene or early Pliocene (Shaffiqullah et al., 1980; Busing, 1990) and in the Pleistocene (DiGiuseppi and Bartley, 1991). The Colorado Paleoriver was diverted from its delta in the Los Angeles Basin to

the Salton trough about 9 Ma (Howard, 1996). The depositional elevation of the Bouse Formation (near the Arizona-Nevada border) is usually cited as at sea level, constraining the time of uplift of the Colorado Plateau, but this is currently in dispute. Bouse Formation sediments and shells show ratios of strontium isotopes intermediate between values expected for marine and freshwater, indicating this area had a mixture of water sources with different strontium isotopes, according to Spencer and Patchett (1997). These authors' contention that the formation was deposited in a lake, possibly at an elevation of 400–700 m, is rejected on the basis of fossil and biogeographic data; the Bouse Formation contained a fauna of foraminifera, barnacles, brackish-water fishes, and marine mollusks (Metzger, 1968; Smith, 1970) that could not have been supported for 3 My by dispersal on birds' feet, as suggested by Spencer and Patchett (1997). The hypothesis that the Bouse Formation was lacustrine (Spencer and Patchett, 1997) has been tested and, by inference, rejected by the absence of any such marine faunas in saline lakes today (Kidwell in Spencer and Patchett, 1997).

Pliocene fluvial connections between the northern pre-Lahontan Basin and the Alvord Basin of Oregon are indicated by geological data (Reheis and Morrison, 1997) and fish distributions (Appendix, numbers 9, 22, 91, 96, 97). DNA divergence data (below; Table 3) suggest that reconnections 0.2 Ma allowed trout populations in these basins to once again mix.

PLIO–PLEISTOCENE.—Connections among the Mono Lake, Owens River, Death Valley, Mohave River, and lower Colorado River drainages are indicated by cyprinodontid fish distributions (Miller, 1948) and geological data (Gale, 1915; Morrison, 1965; G.I. Smith, 1978; Benson et al., 1990). The connection between the Mohave River and the Colorado River basins through Bristol, Cadiz, and Danby Basins lacks support from geomorphology, according to Brown and Rosen (1995), but the connection suggested by present *Cyprinodon* distribution is supported by sedimentary data (Hale, 1985) and by marine or saline-lake foraminifera from cores in Danby and Cadiz dry lakes (Smith, 1960). The foraminifera occur in green clays that are currently within a few hundred feet above or below sea level.

PLEISTOCENE.—Pleistocene connections occurred on a landscape more like that of the present (Figure 13). Additional evidence for exchange between the Lake Bonneville and Virgin River drainages, possibly in the Pleistocene, is seen in *Catostomus clarki* from the headwaters of the Virgin River. These fish have unique predorsal scale and gill-raker counts that increase clinally toward their relatives across the divide in the Bonneville Basin (Smith, 1966). Numerous possible stream captures are associated with the major north-to-south valley west of Hurricane Fault (Averitt, 1964; Anderson and Mehnert, 1979) in southern Utah (along Highway 91). The drainage connection between the Bonneville Basin and the Colorado River drainage is also suggested by intergrades between *Catostomus platyrhynchus* and *C. clarki* in Shoal Creek (Smith and Koehn,

1971), which is in the southernmost part of the Bonneville Basin near the outlet proposed by Ives (1948).

Small headwater-stream captures are required to explain the broad northern distributions of headwater inhabitants, such as *Catostomus platyrhynchus*, *C. discobolus* (Figure 7), *Onco-rhynchus clarki* subspecies (Figure 9), and *Cottus* spp. (Appendix, numbers 124, 125). Numerous examples of northern connections can be recognized on topographic maps and in the field. For example, in Wyoming, two such possible connections may be related to the distribution of *Catostomus platyrhynchus*, *C. discobolus*, and *Cottus bairdi* in the Green, Bear, and Snake Rivers. Willow Creek, formerly tributary to Muddy Creek of the Green River (T.13 N., R.119 W., Ogden sheet, United States Geological Survey (USGS) 1:250,000 series), was captured by the headwaters of the Bear River 11 mi (17 km) southeast of Evanston, Wyoming. Twin Creek, of the Bear River between Fossil Butte and Kemmerer, Wyoming (T.21 N., R.117 W., Ogden sheet), apparently captured the head of Hams Fork of the Green River. We hypothesize that these captures could have carried *Catostomus discobolus* from the Green River drainage to the Bear River, from whence they could have transferred to the Snake River at Soda Springs (Bright, 1967) and to the Weber River in upper Chalk Creek (Hansen, 1969, 1985).

MITOCHONDRIAL DNA EVIDENCE FOR THE TIMING OF PHYLOGENETIC AND HYDROGRAPHIC EVENTS

Analysis of DNA divergence data from fishes offers a means of constraining ages of barriers and uplift in the Great Basin. Estimated rates of evolution of mtDNA genes in Cyprinidae, Salmonidae, and Cyprinodontidae (Figure 14) vary from about 0.5% sequence divergence per one million years in salmonids to about 1% per one million years in cyprinids and cyprinodontids. These values are similar to those reported for snails of the marine gastropod genus *Nucella* (see Collins et al., 1996) and for goodeid fishes (Webb, 1998) but differ from the estimate of Martin and Palumbi (1993). The relative-rate tests (e.g., Table 2) show standard deviations of 10%–25% of the mean values of percent sequence divergence, or roughly 2–5 My for mean ages of 7–38 My (Table 2) for basal branches in the cyprinid data. Standard deviations are 15%–30% in the salmonid data, allowing a rough idea of the imprecision of the estimates. These are overestimates of rates of molecular change because the fossil ages in the denominators of the rate calculations are underestimates. If the rates are underestimated by 10%–30%, elapsed times inferred from rates of molecular change are expected to be underestimates (by as much as 0.5–1.2 My in 4 My for spinedaces, for example). This means that the connection indicated by the Snake River *Snyderichthys* relationship to the Virgin River *Lepidomeda* (percent sequence divergence = 4%) probably occurred within the range of 4–5 Ma.

In general, divergence times based upon the rates calculated herein are old, as predicted by Minckley et al. (1986). Great Basin cyprinids in the sister clade to *Phoxinus* of eastern North America differ from *Phoxinus* by an average of 22%

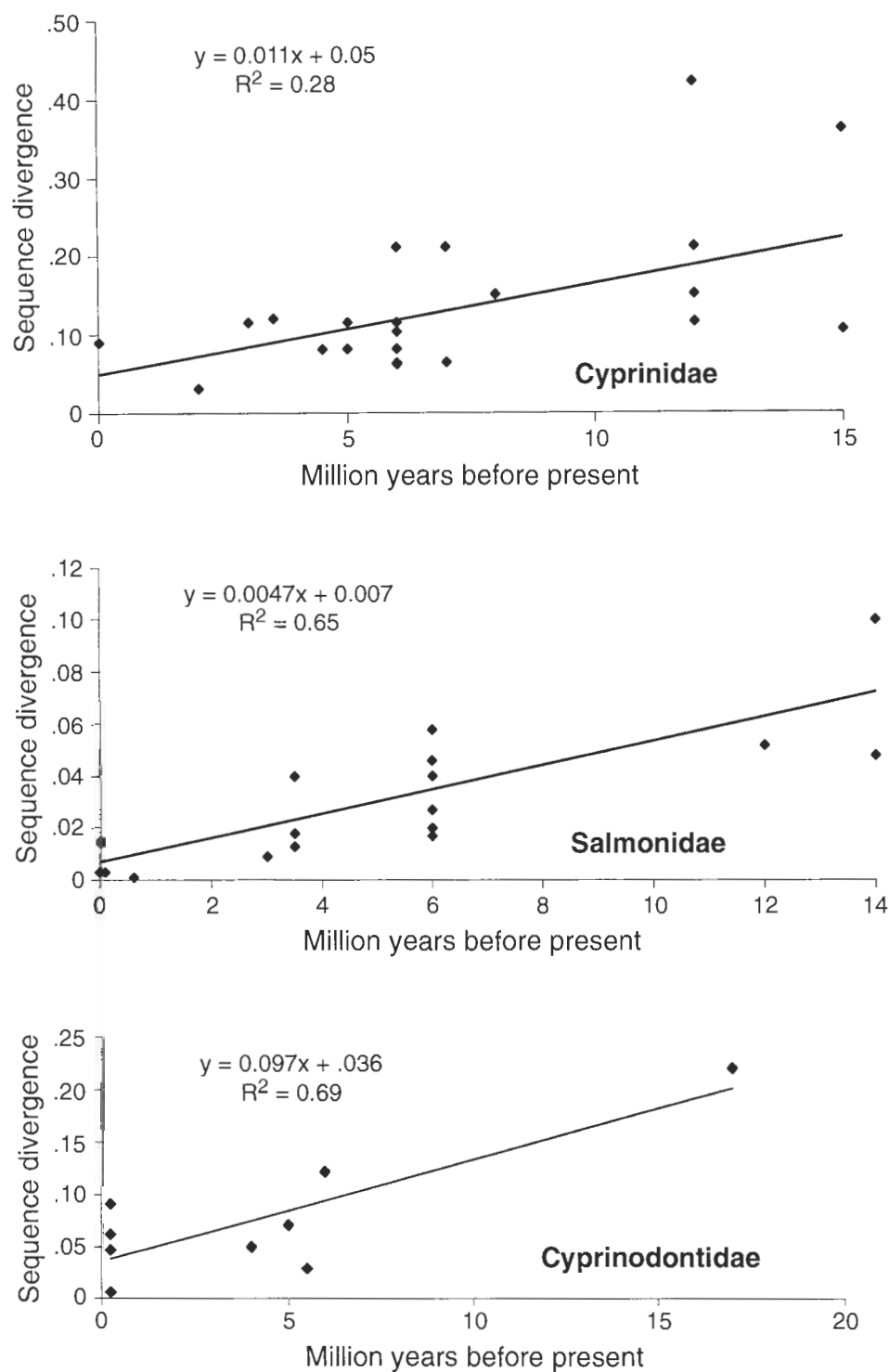


FIGURE 14.—Rates of molecular change in Great Basin and Snake River plain Cyprinidae, Salmonidae, and Cyprinodontidae. Estimated ages of fossils are given in the Appendix and Table 5. DNA sequence divergences are from Tables 2–5; R^2 is an estimate of the percent of the variance explained by the regression.

sequence divergence (Table 2), implying that separation occurred 22 Ma, or in the early Miocene. *Rhinichthys osculus* from the Virgin River and *R. atratulus* of eastern North America differ by 22%. *Snyderichthys* and the *Lepidomeda* group

differ from *Semotilus* of eastern North America by 20%. Closer relatives across the continental divide generally differ by less. For example, *Clinostomus* and *Richardsonius* differ by 12% sequence divergence, and eastern and northern North

TABLE 5.—Fossil cyprinid, salmonid, and cyprinodontoid taxa and ages of samples of first appearances used in the estimations for the rates of molecular change in Figure 14. Fossil taxon numbers correspond to numbers in the Appendix; unnumbered taxa are from outside of the Great Basin. Ages in parentheses are additional fossil records for that taxon. (Fm. = formation.)

Fossil taxon	Sister taxon	Age (My)	% seq. div.
CYPRINIDAE			
1. <i>Lavinia</i>	<i>Mylopharodon</i>	6 (3.5, 3)	8.1
2. <i>Lavinia</i>	<i>Mylopharodon</i>	5 (3)	8.1
3. <i>Lavinia</i>	<i>Mylopharodon</i>	6	8.1
5. <i>Mylopharodon</i>	<i>Siphateles</i>	12	15.0
5. <i>Mylopharodon</i>	<i>Lavinia</i>	4.5	8.1
5. <i>Mylopharodon</i> ?	Eastern minnows	12	42
6. <i>Siphateles</i>	<i>Gila</i>	6 (6)	11.5
6. <i>Siphateles</i> ?	Eastern minnows	15	36
7. <i>Siphateles</i>	<i>Gila</i>	3	11.5
8. <i>Siphateles</i>	<i>Gila</i>	6 (6)	11.5
9. <i>Siphateles</i>	<i>Gila</i>	3 (3)	11.5
10. <i>Siphateles bicolor obesa</i>		2 (0.6)	3.1
14. <i>Siphateles</i> sp.	<i>Mylopharodon</i>	8	15.0
15. <i>Siphateles</i> sp.	<i>Gila</i>	5 (3, 1)	11.5
23. <i>Gila a. atraria</i>	<i>Gila atraria</i> subsp.	0.01	0.9
25. <i>Klamathella</i>	<i>Gila</i>	6	6.2
26. <i>Acrocheilus</i>	<i>Klamathella</i>	6	6.4
26. <i>Acrocheilus</i>	<i>Klamathella</i>	7	6.4
27. <i>Gila</i>	<i>Siphateles</i>	12	11.5
28. <i>Gila</i>	<i>Siphateles</i>	12	11.5
29. <i>Gila</i>	<i>Siphateles</i>	12	11.5
<i>Gila</i> spp.	<i>Ptychocheilus</i>	6	10.3
30. <i>Ptychocheilus</i>	<i>Gila</i>	15 (6, 6, 8)	10.4
37. <i>Richardsonius</i>	<i>Clinostomus</i>	3.5	12.0
56. <i>Mylocheilus</i>	<i>Richardsonius</i>	7	21
57. <i>Mylocheilus</i>	<i>Richardsonius</i>	6	21
58. <i>Mylocheilus</i>	<i>Richardsonius</i>	12	21
SALMONINAE			
87. <i>Salvelinus</i>	<i>Hucho</i>	14	4.8
88. <i>Oncorhynchus</i>	<i>O. clarki</i> + <i>O. mykiss</i>	14	10
89. <i>O. clarki</i> (Truckee Fm.)	<i>O. mykiss</i>	6	4
90. <i>O. clarki</i> (Ft. Rock Basin)	<i>O. mykiss</i>	3.5	4
91. <i>O. clarki</i> (Honey Lake)	<i>O. mykiss</i>	3.5	4
92. <i>O. clarki</i> (Carson Sink)		3.5	1
92. <i>O. clarki</i> (Mopung Hills)		3	1
92. <i>O. clarki</i> (Humboldt River Canyon)	<i>O. clarki</i>	0.7	0.1
97. <i>O. clarki</i> (Whitehorse Basin)	<i>O. clarki</i>	0.15	0.1
97. <i>O. clarki</i> (Sunshine Amphitheater)	<i>O. clarki</i>	1	0.1
98. <i>O. clarki</i> (Sevier Basin)	(Snake River)	0.01	1.3
98. <i>O. clarki</i> (Trout Creek)	(Sevier River)	0.01	1.0
<i>O. nerka</i> ¹	<i>O. gorbuscha</i>	6	5
<i>O. keta</i> ¹	<i>O. gorbuscha</i>	6	3
<i>O. rastrosus</i> ¹	<i>O. nerka</i>	12	5
<i>O. keta</i> ¹	<i>O. nerka</i>	6	6
CYPRINODONTOIDEI			
<i>Chapalichthys encaustus</i> ²	<i>Chapalichthys pardalis</i>	0.25	0.6
<i>Ameca splendens</i> ²	<i>Xiphophorus variatus</i>	0.25	4.7
<i>Allophorus robustus</i> ²	<i>Ameca</i> , etc.	0.25	6.2
<i>Goodea atripinnis</i> ²	<i>Ataeniobus. toweri</i>	0.25	9.1
<i>Girardinichthys multirad</i> ²	<i>G. viviparus</i>	5.0	7.1
<i>Tapatia</i> ²	other <i>Girardinichthyini</i>	6.0	12.2
111. <i>Cyprinodon brevirostris</i>	<i>C. spp.</i>	5.5	2.9
113. <i>Empetrichthys erdisi</i>	<i>Crenichthys</i>	4.0	7.0
122. <i>Fundulus lariversi</i>	Goodeidae	17	22

¹Data from G.R. Smith (1992a).

²Data from M.L. Smith (1980) and Webb (1998).

American *Couesius* differ from *Lepidomeda* by 16% (Dowling et al., 2002), implying that separations occurred in the early to middle Miocene. Great Basin *Gila* differ from Colorado River and Rio Grande *Gila* by 4%–9% (except for northern *Gila atraria*, *G. jordani*, and *G. cypha*, which differ by 0.4%–1.1% sequence divergence, implying there have been relatively recent introgressive transfers of mtDNA; Table 2). Similarly, Great Basin *Gila* and their relatives in the Colorado River, Rio Grande, Rio Yaqui, and in waterways in nearby valleys in the Basin and Range Province of northern Mexico differ among themselves by 5%–9%, implying lower elevations and more connections existed to the south 5–9 Ma (Table 2; Dowling, unpublished data). Great Basin *Gila* differ from Columbia–Snake *Acrocheilus* and *Klamathella* by 6% sequence divergence, but Great Basin *Siphateles* differ from the same taxa by 10%–11%, implying separation occurred well back in the Miocene. Differences between conspecific populations of *Gila* and *Snyderichthys* within the Bonneville Basin range up to 2.4%, indicating subspecific divergence began in the late Pliocene.

Populations of *Oncorhynchus clarki* (cutthroat trout, Table 3) differ from *O. mykiss* (rainbow trout and redband trout) by about 4% sequence divergence, implying separation occurred about 8 Ma (assuming rates of molecular evolution of about 0.5% sequence divergence per 1 My). Populations of *Oncorhynchus clarki* in the Great Basin (except for Deaf Smith Creek and Bear River) differ from populations of the west slope (Columbia River) and the Snake–Yellowstone–Bear Rivers by 1%–2% sequence divergence, implying separation occurred about 4–2 Ma. Bonneville Basin populations are heterogeneous. The Deaf Smith Creek (northern Bonneville) population differs from all other trouts by about 2% more than do other Bonneville trout populations (indicating rapid change occurred in the Deaf Smith Creek population because it is not cladistically basal, Figure 10). The Bear River (most northern Bonneville) population differs from the upper Snake River population by only 0.3%–0.4% sequence divergence, which implies separation took place about 0.7 Ma, which is roughly consistent with part of the Bear River chronology of Bouchard et al. (1998). Populations of the Bonneville and Lahontan Basins differ from each other by an average of 2% sequence divergence, implying they have been separated for about 4 My. Outside the Bonneville Basin, variation within basins is usually less than 0.1%. Lahontan Basin populations differ from those from the Oregon Lakes by only 0.1% sequence divergence, implying they have been separated for about 200 Ky.

Great Basin pupfish populations are related to *Cyprinodon macularius* and its relatives of the Colorado River and Mexico (Echelle and Dowling, 1992; Echelle and Echelle, 1993; Figure 11, Table 4). The Owens pupfish, *C. radiosus*, is a member of the *C. macularius* clade but not the Death Valley clade; *C. radiosus* differs from *C. macularius* by 2.7%–2.8% sequence divergence. Death Valley pupfishes differ from *C. macularius*

and *C. radiosus* by about 3% sequence divergence, implying separation occurred about 3 Ma. *Cyprinodon fontinalis* of Mexico may be a member of the Death Valley clade. These relationships require multiple connections between the Death Valley system and drainages in Mexico, through the Colorado River drainage in the Plio–Pleistocene. *Cyprinodon salinus* of the Salt River in Death Valley differs from other Death Valley pupfishes by 1.3% sequence divergence, implying separation took place a little more than 1 Ma. *Cyprinodon diabolis* and several subspecies of *C. nevadensis* form a clade whose populations differ from each other by about 0.2%–0.6% sequence divergence, implying separations occurred 0.2–0.6 Ma. Miller (1948:85–86) concluded that the divergences of *C. salinus*, *C. diabolis*, and *C. nevadensis* date from about the middle Pleistocene, which is consistent with the molecular differences given above (Table 4). For divergence of some Death Valley populations to have been as rapid as hypothesized by Hubbs and Miller (1948b:82)—as short as 10 Ky—would require unrealistically high rates of sequence divergence.

SPECIES DIVERSITY

Fishes of the Great Basin are not diverse, except in endemic species and subspecies (Hubbs and Miller, 1948b). Most of these taxa are explainable as relicts of repeated cycles of extinction or introgression during dry periods between Pleistocene pluvials. The subspecies are the product of rapid change in morphology in isolated, small populations in rapidly changing environments (Hubbs and Miller, 1948b). But low diversity in a landscape so divided by barriers (permitting divergence and recolonization following divergence) is not consistent with most hypotheses about geographic and climatic control of speciation processes (Hubbs and Miller, 1948b; Mayr, 1963; Vrba, 1993). Great Basin fossil and Holocene fish data indicate, however, that periods of aridity and insularity, coupled with high barriers that prevent recolonization after local extinctions, have eliminated more species than were produced by the numerous stages of isolation; therefore, the processes that cause species divergence have not matched extinction at the spatial and temporal scales of isolation that have occurred in the Great Basin. High extinction rates have been predicted for small, isolated populations (MacArthur and Wilson, 1967; Jablonski, 1980). To determine whether speciation has been influenced by these factors, we considered the processes that have operated in Great Basin fish populations in relation to isolation by pluvial cycles.

Two unusual kinds of data lend themselves to empirical analyses of these two problems. First, the Basin and Range Physiographic Province is divided into dozens of pseudo-replicated fish habitats isolated by mountain ranges, making a highly constrained physiographic region. This permitted us to trace lineages with rather well-controlled histories. Second, the region has a more detailed fossil fish record (Figure 1) than is available for most modern fish faunas, and this record is supported

by a reasonably well-known stratigraphic context (e.g., Benson et al., 1990; Morrison, 1991; Oviatt et al., 1992) and by mammalian stratigraphy (e.g., Stirton, 1936; Lindsey et al., 1984; Lundelius et al., 1987; Repenning, 1987; Tedford et al., 1987; Woodburne, 1987). These circumstances enabled us to begin to address some of the most difficult problems in evolutionary biogeography: Over what time scales do speciation processes occur? How long does it take for differentiation of races, subspecies, and species to occur in isolation? Are the rates of differentiation interval-dependent (Gingerich, 1986), i.e., is the concept of a general rate inappropriate (Bookstein et al., 1978; Bookstein, 1986; Bell, 1994)? Consideration of questions about species and their origins requires a species concept that is open to testable hypotheses concerning processes of origination.

SPECIES CONCEPTS AND SPECIATION HYPOTHESES.—Three species concepts stand out as most relevant to models of freshwater fish speciation in the Great Basin: phylogenetic, biological, and evolutionary. The phylogenetic species concept (Cracraft, 1983) focuses on diagnosable, monophyletic, and irreducible units that maximize the recognition of biotic diversity. Many more phylogenetic species could be recognized than are currently acknowledged in the Great Basin. The phylogenetic species concept is often rejected because its lower limits are not well constrained (Mishler and Donoghue, 1982) and because many species are not monophyletic. Local demes, such as the subspecies and races of *Cyprinodon nevadensis*, *Siphateles bicolor*, and *Rhinichthys osculus*, could be recognized as species under this model. Moritz et al. (1995) argued for use of mutually and reciprocally unique differences as species criteria. This concept requires no information about time, monophyly, or reproductive isolation, so it is independent of evolution of reproductive isolation. The addition of reproductive and historical tests to proposed species enables more complete evaluation of speciation models.

The biological species concept (Mayr, 1963) recognizes groups of populations that are reproductively isolated from other such groups. The focus on reproductive isolation makes this concept central to most speciation process models. Species so defined often contain geographically variant populations, so that in the Great Basin the concept is realistic and objective but is operational only by inference. This definition is sometimes applied too restrictively to accommodate some Cyprinidae, Catostomidae, and Salmonidae, for which there is evidence of gene flow between historically well-differentiated lineages that diverged several million years ago (Smith, 1992a). The biological species concept is improved for our purposes by integration with the ecological species concept of Van Valen (1976, 1988), that is, accommodation of limited gene exchange between long-term, ecologically independent lineages.

The evolutionary species concept (Simpson, 1951; Wiley, 1981; Mayden and Wood, 1995) requires evidence that lineages have separate evolutionary histories, usually diagnosed in a cladistic context. This concept does not require (or rule

out) evidence for reproductive isolation as evidence for lineage independence. The evolutionary species concept is applicable to Great Basin fish lineages to the extent that introgressed but still-separate lineages are not excluded because of non-monophyly or temporary lapses in independence.

The time required for acquisition of genetically based ecological or reproductive isolation as a guarantor of lineage independence is a matter of special concern in the study of speciation in the Great Basin because of the large number of diagnosable, but possibly ephemeral, allopatric populations. Western North American fishes show a high degree of allopatry, but they also provide unusually frequent examples of gene exchange between species of long-standing independence (Hubbs, 1955). Great Basin species of minnows, suckers, trouts, pupfishes, and sculpins are especially consistent with species concepts and origination models that require reproductive independence, but not necessarily isolation. Modest introgressive influence does not contradict this definition, if the morphologically and ecologically different lineages are not amalgamated through hybrids with high fitness. Reproductive independence and reproductive isolation are often assumed to be synonymous and mutually required for species recognition, but in many species, it is worth making a distinction. Evidence for introgression is usually taken to be evidence against independence (by zoologists, not botanists; Wagner, 1983; Rieseberg and Wendel, 1993), but if forms are ecologically different enough to be disruptively selected, introgression does not necessarily reduce two lineages to one.

For example, the ecologically distinct pairs *Catostomus ardens* and *Chasmistes liorus* of Utah Lake belong to clades that diverged 3–6 Ma. Introgression occurred in the Provo River at the time of the drought in the early 1930s (Miller and Smith, 1981), but morphological stability of *C. ardens* and ecological persistence of (modified) *C. liorus* indicate sufficient reproductive separateness between these forms to warrant species rank. In contrast, some pairs of populations of *Siphateles bicolor obesus* and *S. b. pectinifer* in the Lahontan Basin failed to stay separate through recent times (Hubbs and Miller, 1948b). These different outcomes are ecology dependent (Van Valen, 1976, 1988) in that the reproductive isolation is maintained only by spawning-site selection based upon ecological characteristics—depth, current, light, temperature, and substrate. Evolution of lineage independence, therefore, is partly a function of ecological context (Smith, 1992a; Smith et al., 1995). The introgression hypotheses of Hubbs and Miller (1948b) and Smith (1992a) suggest a Pleistocene history of alternation between habitat-rich pluvials and habitat-poor, arid interpluvials, which could have resulted in cyclic adaptation to special habitats in wet times, followed by selection of morphologically generalized phenotypes during times of reduced habitat diversity. The result is introgressive destruction of some (but not all) independent lineages.

We therefore define species as lineages whose separate history can be reasonably inferred from diagnostic morphological,

ecological, genetic, or behavioral apomorphies. This definition recognizes that species are individuals (Ghiselin, 1974, 1997), and it is meant to be consistent with Ghiselin's general definition (1997:99): "Biological species are populations within which there is, but between which there is not, sufficient cohesive capacity to preclude indefinite divergence." Our wording acknowledges extrinsic properties and emphasizes history. It might also be peculiarly ichthyological—D.S. Jordan (quoted by Joseph Grinnell, 1924:225) said that "a species is not merely a group of individuals distinguished from other groups by definable features;" it is "a kind of animal or plant which has run the gauntlet of the ages and has persisted." The intrinsic bases for maintaining historical lineage separateness may be ecological (different habitats), reproductive (different times or places of spawning), or developmental (different genes for growth), but they are ultimately genetic and controlled by long-term selection (Fisher and Ford, 1947; Wright, 1948). The traits that we focus upon herein are associated with reduced hybrid fitness because of high mortality or low fertility (Dowling et al., In prep.). Tests of intrinsic reproductive separation are usually inferred from (1) the presence or absence of traits unique to sympatric relatives, (2) apomorphic courtship displays, (3) assortative mating, (4) failure to produce fertile or viable offspring, or (5) reduced fitness of hybrid products. Tests of long-term persistence require paleontological or molecular biogeographic data that provide a time context in which to evaluate persistence or stability for a period longer than a post-glacial fragment of a glacial cycle. We suggest that molecular divergence measures can contribute to this test, although a sharp, defining demarcation in time or sequence divergence is not suggested. The criteria presented above provide appropriate evidence for accepting or rejecting species assignment under both the evolutionary and the biological species concepts. These considerations provide a context for analyzing the temporal scale of morphological and genetic differentiation in relation to speciation.

The above definition and the patterns of Great Basin fishes through geologic time suggest avoidance of the chronospecies concept, which is popular in paleontology but incompatible with cladistic, evolutionary, or biological views of species (Krishtalka and Stucky, 1985; Ghiselin, 1997). Great Basin species are interpretable as individuals that may change through time, sometimes anagenetically, and sometimes through recombination of genes from related populations. In either case, the individuality of ancestral-descendant lineages through time is paramount (Ghiselin, 1974, 1997), and it seems unhelpful to the study of speciation to change lineage names to indicate anagenetic changes. To name chronological species recognizes only stratigraphic diversity, not species diversity. Similarly, it seems unhelpful to change the name of a sister taxon that has given rise to a peripatric daughter taxon without any change in the morphology of the original population (Bell, 1979).

SPECIES FORMATION IN THE GREAT BASIN.—The Great Basin fishes are a product of cycles of expanded and contracted habitats, resulting in cycles of differentiation of local populations but only modest persistence of lineages through time. Here the speciation process involves three steps (Smith et al., 1995): (1) separation of populations by hydrographic or habitat barriers (or microhabitat difference in lakes); (2) accumulation of genetic differences in growth, development, physiology, ecology, or behavior; and (3) accumulation of some minimum combination of genetically based differences sufficient to cause hybrids to suffer reduced fitness. Operationally, the products of these process are recognized when lineage independence seems reasonably supported by reciprocally nonoverlapping molecular, morphological, or ecological apomorphies that indicate an intrinsic basis for lineage separateness. Confidence in and predictions from these hypotheses are subject to tests by paleontological or biogeographic circumstances that indicate persistence through more than one environmental cycle.

The Cenozoic tectonic and Pleistocene hydrographic history of the Great Basin created hundreds of allopatric isolates with the potential to become species, as demonstrated by Hubbs and Miller (1948b) and Hubbs et al. (1974). We conclude, however, that the same conditions (small isolates) and processes (long isolation and short cycles of habitat fluctuation) that caused the initial differentiation also caused extinction of the majority of potential species. Evidence of this extinction is seen in the declining late Cenozoic fish diversity, depauperate local faunas, and absence of the vast species numbers expected from scores of so-called "species-pump" cycles.

Examples of surviving vicariant pairs in the Great Basin are nevertheless notable. They include *Lepidomeda albivallis* and *L. altivelis* in the White River Valley and in Pahrnagat Valley, Nevada; *Richardsonius egregius* and *R. balteatus* in the Lahontan and the Bonneville–Columbia Basins; *Catostomus tahoensis* and *C. fumeiventris* in the Lahontan and Owens Basins; *Cyprinodon salinus*, *C. milleri*, *C. nevadensis*, and *C. diabolis* in the Death Valley system; *Crenichthys baileyi* and *C. nevadensis* in the White River valley and in Railroad Valley; *Empetrichthys latos* and *E. merriami* in Pahrump Valley and Ash Meadows; and *Cottus extensus* and *C. echinatus* in Bear Lake and Utah Lake. Most of the other species in the Great Basin have sister taxa outside the basin or have complex distribution patterns requiring dispersal. Examples of stages of differentiation similar to the above are found among the subspecies and races of *Siphateles bicolor*, *Rhinichthys osculus*, *Gila atraria*, and *Oncorhynchus clarki*. These forms are early and perhaps temporary examples of vicariant speciation, as described above. Our DNA divergence data and the hypothesis that speciation usually involves the long-term accumulation of multiple genetic differences suggest that, on average, species-level differentiation (beyond the subspecies and races of Hubbs and Miller) requires a longer time than the duration of the Pleistocene.

Lacustrine speciation requires special explanation. Examples include the species of *Prosopium* in Bear Lake and the Bonneville Basin, and *Siphateles bicolor pectinifer* in the Lahontan Basin. The trophic and lacustrine adaptations of these sympatric forms indicate that they might have differentiated in intralacustrine micro-allopatry (Smith and Todd, 1984) involving evolution of different habitats and spawning times. Independent evidence suggests that intralacustrine speciation is much more rapid than speciation in most other circumstances (Mayr, 1984; McCune et al., 1984; Smith et al., 1995), possibly because it is driven by competitive selection (Rosenzweig, 1978). Variability also might be enhanced by relaxed selection during lake transgression and population expansion (McCune, 1990).

There is a widely cited hypothesis that lacustrine speciation is driven by cyclic allopatry, with low stages that separate allopatric populations, which diverge, and high stages, which foster dispersal and widespread sympatry (e.g., Mayr, 1963; McCune et al., 1984). The history of the Great Basin includes numerous pluvial cycles (dozens, if pluvial cycles tracked glacial cycles) during the last 3 My (Imbrie and Imbrie, 1979; Benson et al., unpublished data; G.I. Smith et al., unpublished data). The pattern of species abundance and distribution in Great Basin fishes does not conform to the lacustrine fluctuation model of lacustrine speciation (Mayr, 1984; Smith and Todd, 1984) because extinction, not speciation, has dominated Great Basin history (Smith, 1978), perhaps because the arid parts of the cycle have been so extreme.

The fossil and molecular evidence for an ancient presence (a criterion suggested by Ricklefs and Schluter, 1993) of most of the species in the Great Basin also suggests that extinction has been more frequent than species production. The abundance of races and subspecies in the Great Basin suggests that frequent origin and extinction jointly act on populations with limited ranges. Species with stable habitats or large geographic ranges, by contrast, tend to be long-term survivors (Jablonski, 1980).

The pattern of morphological change through time, if viewed on the million-year time scale, would appear to be consistent with the hypothesis that most morphological changes in species occurred at the time of initial divergence (Stanley, 1975; Gould and Eldredge, 1977). Viewed on the thousand-year time scale, we see early morphological response to changing environments, but slow accumulation of characters that may be capable of sustaining long-term individuality.

TEMPORAL SCALE OF SPECIES DIFFERENTIATION IN THE GREAT BASIN.—These cases suggest a model in which Great Basin fish differentiation was distributed broadly across pluvial cycles of the last 3 My. Through time, some fraction of the new forms went extinct, and some species and subspecies introgressed into relatives during extinction episodes. Some of these diverged again during pluvial and early postpluvial episodes. The net result is abundant geographic variation cycling through time, as seen in the fossil record, combined with low species diversity, as seen in Great Basin fishes today (Miller, 1959).

The fossil record indicates that throughout the million-year time scale, net changes have been slow. Geographic variation shows that during the thousand-year time scale, some morphological changes in oligogenic and ecophenotypic traits have been rapid (Hubbs and Miller, 1948b; Bell, 1994). It is possible that bony characters seen in the fossil record are multigenic and evolve more slowly than oligogenic meristic, color, and shape characters that differentiate subspecies. It is also likely that body shape, scale, and fin characters fluctuate, perhaps ecophenotypically, which is consistent with the random-walk hypothesis (Bookstein et al., 1978). Fluctuating variations observed during a time scale of hundreds of years (Bell and Haglund, 1982; Bell et al., 1985; Bell, 1994) and decades support this hypothesis (Figure 12). Small, rapid changes are expected in short-term studies, in contrast to slow changes expected in long-term studies (Gingerich, 1986), in part because genetic variation is consumed by selection (Lewontin, 1974).

These differences in amounts of change as a function of time are observed in empirical studies in the laboratory as well as in comparisons of paleontological rates (Gingerich, 1986). Random fluctuation was not one of the hypotheses considered by early students of Great Basin fishes: Hubbs (1940:211) saw "orderly adjustment under the control of environment" not "aimless wandering of genes through the organic world." Studies of morphological fluctuations in the fossil record (Figure 12; Bookstein et al., 1978; Chernoff, 1981; Bookstein, 1986; Bell, 1994) and complex biogeographic patterns in the Great Basin suggest a model of rapid adaptive response to changing environments but minimal long-term trends because of the high amplitude and periodicity of the fluctuations.

Conclusions

The Great Basin fish fauna is the most depauperate ichthyofauna in North America, despite being situated on a landscape ideal for allopatric speciation. Comparison of morphological subspecies differences (Hubbs and Miller, 1948b; Hubbs et al., 1974) with paleontological studies of populations through time indicates that abundant, newly differentiated forms usually fail to become long-term members of Great Basin biodiversity. This fauna has not significantly diversified despite repeated Pleistocene fluctuations in lake levels. The absence of the diversity predicted by repeated environmental change leads to two conclusions: (1) extinction of small populations is a more potent long-term force than speciation in fluctuating environments, such as occurred in the Pleistocene Great Basin; and (2) speciation processes are favored in small populations (Wright, 1940a; Mayr, 1963; Gould and Eldredge, 1977), but during a time scale of thousands of years, most of this diversity becomes extinct if individuals in small populations cannot disperse among drainages.

A related aspect of these fishes is that western salmonids, catostomids, cyprinids, and cyprinodontids are unexpectedly lacking in intrinsic reproductive isolation among morphologi-

cally and ecologically differentiated lineages, some of which have separate evolutionary histories going back several millions of years (Smith, 1992a). Fluctuations in abundance have caused frequent hybridization (Hubbs and Miller, 1943; Hubbs, 1955). The frequent exchange of genes through introgression appears to have maintained some genetic compatibility, even as it provided variation for adaptations to environmental change.

The extreme isolated allopatry and resulting divergence of Great Basin fishes permit some calibration of the chronology of hydrologic history of basins, as sought by Hubbs and Miller. Molecular divergence estimates, in conjunction with ages of fossil ancestors, enable the calculation of DNA divergence-rate estimates in salmonids (0.5% per 1 My) and in cyprinids and cyprinodontids (1% per 1 My). These results permit percent sequence divergence to be used to calculate a rough chronology of hydrologic barriers between individual basins, groups of basins, and drainages neighboring the Great Basin. The Rocky Mountain barrier between Great Basin and eastern North American fishes was crossed at low elevations multiple times between 22 and 12 Ma, according to cyprinid sequence divergences. Major connections among Great Basin, Colorado River,

Rio Grande, Rio Yaqui, and adjacent drainages in the Basin and Range Province of northern Mexico date from 9 to 5 Ma, based upon cyprinid divergences. Great Basin and Columbia–Snake divergences of cyprinids imply that separations occurred early, 11–6 Ma, but that many reconnections occurred during the interim. Two levels of differences between lowland and upland taxa of the Lahontan and Bonneville Basins imply that major confluences existed prior to 12–6 Ma and minor headwater connections occurred 4–0.2 Ma. Estimates based upon trout DNA sequence divergences imply that the Lahontan Basin headwaters were connected to the Columbia River drainage about 0.2 Ma, but Lahontan Basin populations were connected to each other more recently than 0.2 Ma. The Bear River populations were connected to the Snake River populations 0.3 Ma, but the trouts of the Bonneville and Lahontan Basins were connected 4–2 Ma. Cyprinodontoids of the Death Valley system were connected to the lower Colorado River basin and to Mexico several times in the last 2–3 My and were among basins in the Death Valley system during the last 0.1–1.3 My. In summary, paleontological and molecular evidence indicates that most Great Basin fish lineages are older than previously thought.

Appendix

The fish species and subspecies of the hydrographic Great Basin, both fossil and Holocene, are listed below in approximate phylogenetic sequence and are numbered to correspond to references to them in the text, tables, and figures. Forty-one forms known only from fossils are indicated by a dagger (†). An asterisk (*) indicates that the account of the Holocene lineage contains a pertinent fossil record.

CYPRINIDAE

Western Chub Group

Mylopharodon–*Lavinia*–*Hesperoleucus* Subgroup

1. †*Lavinia* sp. (Secret Valley hitch). This small species is diagnosed by pharyngeal teeth with corrugated grinding surfaces and by dentaries with flared lateral edges (Smith, 1975, fig. 19B). *Idadon* of the Snake River Plain is herein interpreted as a synonym of *Lavinia* of the Great Valley ("1" in Table 2). *Idadon* and *Lavinia* share the unique features of corrugated pharyngeal teeth and flared dentaries, although these features are more extremely developed in *Idadon*. Flared dentaries collected from elsewhere on the Madeline Plains, northeastern California, have been identified as *Lavinia* and *Acrocheilus* by Wagner et al. (1997). The Secret Valley dentaries are more flared than those from the Snake River Plain. Although highly variable, the Secret Valley dentaries are more similar to *Acrocheilus* than to *Lavinia* (Wagner et al., 1997), but they lack the

abrupt angles of *Acrocheilus*. (*Acrocheilus* teeth are not present among UMMZ specimens from Secret Valley.) The Secret Valley fossils are assigned an age of ~3.5 Ma; this assignment was based on their correlation with specimens from the Snake River Plain.

Lavinia + *Hesperoleucus* is the sister group to *Mylopharodon* in the cladogram (Figure 2). *Lavinia* and *Mylopharodon* are known from apparent first appearances on the Snake River Plain about 6 Ma and 4 Ma, respectively; these ages correlate with the sequence divergence value of 8.1% (Tables 2, 5) in Figure 14.

Molecular evidence (Table 2) indicates a sequence divergence of 15% between *Siphateles bicolor* and *Lavinia*. (See number 14, below.)

2. †*Lavinia* sp. (Carson Valley hitch). A partial left dentary from late Blancan sediments (~3 Ma) and three caudal vertebrae from early Blancan sediments (~5 Ma) were collected in Carson Valley by T. Kelly. The dentary is 10.5 mm long and represents a fish about 18 cm in standard length (SL). The specimen is diagnosed as *Lavinia* by the flared gnathal ramus, coronoid process at midpoint of the bone, mesially curved anterior end, and position of eight lateralis pores. The caudal vertebrae are dorsoventrally compressed, with a thick, single longitudinal ridge on the lateral surface of the centrum.

3. †*Lavinia* sp. (Cache Valley hitch). Specimens collected from Cache Valley near Logan, Utah, by J. Stewart Williams of Utah State University, appear to be large *Lavinia*. This conclusion is based upon the slightly corrugated grinding surfaces on

the pharyngeal teeth, the flared dentaries, and the high fin-ray counts. The distinct morphology and the absence of Pliocene indicators with these fossils suggest a pre-Blancan, late Miocene age (~6 Ma). McClellan (1977) reported *Idadon* (herein treated as a synonym of *Lavinia*) from the Junction Hills fauna of the Salt Lake group, near Fielding, Box Elder County, Utah. The fossils appear to be Hemphillian in age by correlation with adjacent faunas. Cyprinids similar to *Lavinia* or *Mylopharodon*, but not to *Gila*, have been collected from the Bear River valley near Georgetown, Idaho, by Sue Ann Bilby and have been deposited in the collections of the Idaho State Museum of Natural History. This record supports the age estimate of 6 Ma assigned to the sequence divergence value of 8.1% in Figure 14.

4. *Hesperoleucus symmetricus* (Baird and Girard) (California roach). This species lives in the Great Basin only in the Warner Lakes system, near Adel, Lake County, Oregon. It is most similar to *Hesperoleucus* sp. in Goose Lake and the Pit River drainage (from where it might have been introduced (Miller, 1959)). Although sometimes placed in *Lavinia* because of protein and molecular similarities, the morphological differences and fossil record suggest that *Lavinia* and *Hesperoleucus* are long-different lineages that share molecular similarity (they differ by only 1.3% sequence divergence) probably because of introgression.

5. **Mylopharodon* Ayres (western chubs). Chubs with molariform teeth occurred in the Great Basin and in the Snake River Plain from the middle Miocene through the Pliocene, and they remain in the Great Valley of California. Fossils of this genus are rare in the Great Basin. †*Mylopharodon*(?) *doliolus* Smith and Kimmel was a large chub with widely spaced, rounded molariform teeth (Smith et al., 1982, fig. 4E). It was placed in *Mylopharodon* because of its molariform teeth, elongate posterodorsal process of the pharyngeal arch, and general shape of the pharyngeal arch. This form is from the Esmeralda Formation in Silver Peak Quadrangle, Nevada, and may be as old as 12 ± 2 My. It lacks the derived characters of all *Mylocheilus* and *Mylopharodon* (of the Snake River Plain, Great Basin, Sacramento Basin, northeastern California, and southeastern Oregon) and, therefore, could represent the stem group leading to *Mylopharodon* and *Siphateles*. *Mylopharodon* lived in the Honey Lake basin (collected by Todd Yeoman of Sierra College) and the Snake River Plain during the Pliocene. †*Mylopharodon hagermanensis* Uyeno first appeared at Hagerman, Idaho, on the Snake River Plain about 4.5 Ma. *Mylopharodon conocephalus* (Baird and Girard) of the Great Valley (number 5 in Table 2) and *Siphateles* (of the Lahontan Basin) differ by 10.2% sequence divergence (Figure 2; Table 2). The Miocene fossil could also be the earliest western relative of eastern cyprinids, from which *Mylopharodon conocephalus* differs by 42% sequence divergence (Table 2; Dowling, unpublished data).

Siphateles Subgroup

6. **Siphateles* sp. (chub). Chubs with a single row of pharyngeal teeth on each arch are widespread in the late Miocene to Holocene fossil record of Nevada. Whole fossils and numerous separate bones similar to *Siphateles* were discovered in Barstovian (middle Miocene, ~15 Ma) beds of Buffalo Canyon, Churchill County, Nevada, by Ron and Zachary Jones. These are the oldest known cyprinid bones in the Great Basin, so they provide an estimate (underestimate) of the time of vicariance with the eastern clade of North American shiners, from which *Siphateles* differs by more than 30% sequence divergence (Table 2; Dowling, unpublished data). A complete but undescribed specimen similar to *Siphateles* is known from the Nevada Test Site in southern Nye County, Nevada. It is believed to be Miocene in age. Several complete specimens and numerous bones are known from the late Miocene beds of the Virgin Valley Formation, Humboldt County, Nevada. Unidentified cyprinid fossils are known from Pine Nut Ridge (Douglas County, late Hemphillian to Blancan) and from the Coal Valley Formation. The late Hemphillian fossils are estimated to be 6 My old and may indicate the branch point with *Gila*, which differs from *Siphateles* by an average of 11.5% (s.d. = 2.2%) sequence divergence (Figure 14; Table 2).

7. †*Siphateles breviararchus* (Cope) (Fort Rock chub). This is the common cyprinid in the Pliocene sediments of Fossil Lake, Lake County, Oregon. It has robust pharyngeals that are similar to those of *Mylopharodon*. It represents a stage of evolution prior to diversification of the *Siphateles bicolor* complex. The date of its divergence from *Mylopharodon* is probably about 10 Ma based on sequence divergence (Figure 14; Table 2).

8. †*Siphateles traini* (Lugaski) (chub). This fossil form, from the late Miocene lacustrine beds in Jersey Valley, Pershing County, Nevada (Lugaski, 1979), is morphologically somewhat similar to *S. bicolor*. The zeolite beds in which *S. traini* occurs suggest that the fish lived in a shallow, saline, alkaline lake of pH 9, much like Pyramid Lake, Washoe County, Nevada, in which *S. b. obesus* currently lives (Lugaski, 1979). Michael Bell and others have collected a large cyprinid from the late Miocene part of the Truckee Formation, near Hazen, Nevada (see number 29, below), with robust proportions and fin-ray counts that suggest a relationship to this group. These late Miocene sites are estimated to be 6 My old (Figure 14).

9. **Siphateles bicolor* (Girard) (tui chub). This polytypic species is widespread in the Lahontan Basin drainage as *S. bicolor obesus*, and it also extends into Oregon's lake basins as *S. b. bicolor*, and into the Harney Lake and lower Columbia River basins, where it has been referred to *S. b. columbianus*. *Siphateles bicolor* is diagnosed by a single row of pharyngeal teeth. Cyprinid bones found in indurated sediments of Pyramid and Winnemucca Lakes and other areas of the Lahontan Basin are probably *Gila bicolor obesus*. Fossils related to this species are

known from the Pliocene of Honey Lake, Lassen County, California, and Mopung Hills, Churchill County, Nevada, and from numerous Holocene Indian middens reported in the archaeological literature. The Blencoe fossils occurred before Pleistocene tectonism began at the Honey Lake site, possibly 3 Ma. Samples from the Lahontan Basin, from the Owens River, Mono Lake, Mohave River, and Oregon Lakes basins, and from the Columbia River, analyzed by Dowling, differ from each other by 3.1% of the cytochrome *b* sequence (Table 2).

Siphateles bicolor obesus is widespread throughout the streams and springs in the Lahontan Basin system, where it typically has 10–19 short gill rakers, a 5–4 pharyngeal tooth formula (Hubbs et al., 1974), and distinctive scales. Many unnamed, geographically distinct forms, in addition to the named taxa summarized below, vary in gill raker number or morphology, scale counts, size, proportions, nuptial characters, and color patterns. For example, Sulfur Spring, in Diamond Valley, Eureka County, Nevada, contains a dwarf form with long gill rakers, complete lateral line, long pectoral fins, and distinctive colors; it is included with *S. b. obesus* because a downstream population has features that are intermediate between it and the Humboldt drainage forms (Hubbs et al., 1974).

Hubbs and Miller (1948b) reported distinct subspecies in the valleys of Lake Dixie and Lake Toiyabe, in Big Smokey Valley, and in Railroad Valley in central Nevada, south of the Lahontan Basin drainage (Figure 4). Another distinct form lived on the east side of the valley of pluvial Lake Toiyabe in Lander and Nye Counties, Nevada, along with *Rhinichthys osculus lariversi* (Lugaski, 1972). (Forms on the west side of the valley were apparently transplanted into the springs around the turn of the century; both populations of *S. bicolor obesus* are now extinct.)

Just about every isolated population of *S. bicolor* in the Oregon Lakes has a distinctive combination of characters involving size, body shape, fin shape, gill raker length and number, and color (Hubbs and Miller, 1948b; Hubbs et al., 1974). *Siphateles bicolor eury soma* (Williams and Bond, 1981) was named from the Guano Basin, Nevada. The Catlow Valley chub in Malheur County and the Guano Valley chub in southeastern Lake County, Oregon, are recognized as *Siphateles bicolor eury soma* Williams and Bond (1981) (Hubbs and Miller, 1948b). *Siphateles bicolor* in the Oregon basins vary from forms with more than 16 gill rakers (Catlow Valley, Guano Lake, and Warner Lakes basins) to forms with fewer than 16 gill rakers (basins of the lower Columbia River, of Harney, Klamath, Fort Rock (Fossil), Alkali, and Summer Lakes, and of Lakes Abert and Chewaucan) (Minckley et al., 1986).

10. †*Siphateles* sp. (chub). Pliocene(?) fossil *Siphateles* from Duck Valley, Washoe County, Nevada, is estimated herein to date from 2 Ma. Specimens like the modern *Siphateles* of the Lahontan Basin occur in Humboldt Canyon below the Lava Creek tephra, which was deposited 665 ± 10 Ka (Izett, 1981; Izett et al., 1992) and the Brunhes–Matuyama geomagnetic reversal, 780 Ka (Baksi et al., 1992). Oregon and Nevada speci-

mens differ by 3.1% sequence divergence (Table 2). G.I. Smith and colleagues of the United States Geological Survey (USGS) recovered a specimen from the Searles Lake core (R.R. Miller, pers. comm. to G.R.S., 1999).

11. †*Siphateles bicolor* subsp. (chub). Gobalet and Negrini (1992) reported a distinct but undescribed fossil form of *S. bicolor* from the Chewaucan Basin of southern Oregon; the form was stated to be more than 10 Ky old. Modern specimens of *Siphateles* from Oregon and Nevada differ from each other by 3.1% sequence divergence (Table 2). Modern representatives in the Chewaucan, Alkali, and Fort Rock Basins (Figure 4) are similar to each other (Hubbs and Miller, 1948b).

12. **Siphateles mohavensis* Snyder (Mohave tui chub). This distinct chub was originally described as a species from the Mohave River in the valley of pluvial Lake Mohave. It has eight anal-fin rays, uniserial teeth, and 18–29 gill rakers. Its numerous gill rakers characterize a plesiomorphic condition retained from its lacustrine ancestor (Hubbs and Miller, 1948b). Otherwise, it is similar to tui chubs (Miller, 1973). Fossils related to this form were reported from sediments of China, Manix, and Searles Lakes by Buwalda (1914), Blackwelder and Ellsworth (1936), and Flint and Gale (1958). Numerous isolated bones collected by D.F. Hewett and D.W. Taylor from Lake Manix beds represent this species and have osteological characters like the *Siphateles* figured by Miller (1973). Teeth and vertebrae recovered by B. Leatham from “Lake Mohave” (also called Soda Lake) north of Baker, California, dated at 20 Ky B.P., are most likely from this species. Late Pliocene tui chub bones associated with *Catostomus* and *Chasmistes* from the White Hills near Airport Lake, Inyo County, California, may be the same as the Soda Lake form.

13. **Siphateles bicolor snyderi* (Miller) (Owens tui chub). This chub inhabits springs and creeks of the Owens River drainage, Inyo and Mono Counties, California. Small lateral line scales, distinctive lateral radii on the scales, few dorsal and anal-fin rays, a distinctively shaped pharyngeal arch, and usually 10–14 gill rakers diagnose this form. It is most similar to *Siphateles bicolor obesus* in the East Walker River, from which Miller (1973) presumed it was derived. Fragments assumed to represent the Owens River *Siphateles* were recovered throughout the Pleistocene Owens Lake core (Firby et al., 1997). Holocene Indian middens along the nearby Alabama Hills in Inyo County, California, contain abundant remains of this tui chub and *Catostomus fumeiventris*, but no other fishes.

14. †*Siphateles* sp., (Mono Basin chub). Pliocene fossil bones from Mono Lake basin and Miocene to Pleistocene sediments of Carson Valley are clearly plesiomorphic *Siphateles*. The dentaries from both sites are similar to each other and are sufficiently distinct from other *Siphateles* to be regarded as a single, different species (see number 15, below; to be described by K. Gobalet). The Mono Basin sample of *Siphateles* now includes hundreds of identifiable specimens. They are similar to *Gila crassicauda* but are different from other *Gila* and other *Siphateles* in the distinct robustness of the anterior ramus of the

dentary and in the anterior position of the dorsal mental foramen; the anterior edge of the coronoid process is angled more posteriorly in *Gila*. The masticatory platform of the basioccipital is similar to *Mylopharodon* in the obtuse angle of the posterolateral processes at the origin of the caudal process; this part of the bone matches *Siphateles* rather than *Mylopharodon*. The pharyngeal arches bear a single row of teeth, which are robust, somewhat rounded, and reach large size (to 9 mm). These teeth indicate the fossil species had a larger maximum size than the modern record of 42 cm in total length for this species (Sigler and Sigler, 1987). We estimate the age of these fossils to be about 8 My old (based upon the morphological differences described here), which places them closer to the branch point with *Mylopharodon* than with *Gila*. A large, straight dentary and molariform pharyngeal teeth attributed to *Mylopharodon* by Miller and Smith (1981) might be large *Siphateles* with long jaws and rounded teeth.

15. †*Siphateles* sp. (Carson Valley tui chub). Abundant Carson Valley materials are known from the early Blanfordian local fauna, the late Blanford Fish Spring Flat local fauna, and the early Irvingtonian Topaz Lake local fauna, Douglas County, Nevada. They are distinctive in their robust and posteriorly angular pharyngeals, somewhat like the Mono Basin forms. The dentary shows a more anterior position of the dorsolateral mental foramen than other forms, except those from Mono Basin. The masticatory plates of the basioccipitals are rounded ventroposteriorly, like fossil *Siphateles* from the Mono Basin and Humboldt River canyon and from Holocene forms from some Lahontan Basin localities and the Sacramento River drainage. The Carson Valley forms are estimated to have lived 5, 3, and 1 Ma.

16. **Siphateles bicolor pectinifer* (Snyder) (lake minnow). This lacustrine tui chub was described by Snyder (1917a) and placed in the distinct genus *Leucidius*. It can be distinguished by its long, numerous gill rakers (29–36) and by its usually 5–5 pharyngeal-teeth pattern. It is sympatric with *S. obesus* (Snyder, 1917a; Hubbs et al., 1974:143–150). Extensive introgression has eliminated recognizable individuals of this form in Eagle Lake and has reduced its distinctiveness in Lake Tahoe, Walker Lake, and Pyramid Lake. The presence of hybrid pharyngeals in ancient Indian middens (Hubbs, 1961; Smith, 1985) is evidence that the parental forms hybridized but maintained their differences for thousands of years (Hubbs, 1961). Remnant populations of *S. b. pectinifer* in different, unconnected habitats suggests that the ecologically significant differences are genetically based (Hubbs, 1961; Hubbs et al., 1974).

17. *Siphateles bicolor vacceiceps* (Bills and Bond) (Cowhead Lake tui chub). This unique population was discovered by Hubbs and Miller (1948b) in Cowhead Lake, Modoc County, California. It is characterized by its small size (less than 12 cm SL), numerous, short gill rakers (19–25), and small scales. It is most similar to the unnamed chub in Warner Valley (to which Cowhead Lake was tributary in pluvial times), but that form has longer gill rakers (Bills and Bond, 1980).

18. *Siphateles bicolor newarkensis* (Hubbs and Miller) (Newark tui chub). This chub is the only native fish in the springs of the main basin of pluvial Lake Newark, in White Pine County, Nevada. It is characterized by having few, short, thick gill rakers, a usually complete supratemporal canal, long pectoral fins, and small size (less than 10 cm SL) (Hubbs and Miller, 1972; Hubbs et al., 1974).

19. *Siphateles bicolor euchilus* (Hubbs and Miller) (big-mouth tui chub). This is the sister form to *S. b. newarkensis*, with which it shares many features. It is found in springs of Fish Creek (Little Smokey) valley in the southwestern part of the valley of pluvial Lake Newark (southeast corner of Eureka County, Nevada). It is characterized by relatively large size (10–15 cm SL), especially anteriorly; large fins, especially the pectorals; and large scales (Hubbs and Miller, 1972; Hubbs et al., 1974).

20. *Siphateles bicolor isolatus* (Hubbs and Miller) (Clover tui chub). This represents one of two species found in Independence Valley, Elko County, Nevada, in the valley of pluvial Lake Clover. *Siphateles b. isolatus* is small, with intermediate-length gill rakers reduced to about 11. It shares characteristics with *S. b. newarkensis* and *S. obesus* of nearby Bishop Creek of the Lahontan Basin drainage (Hubbs and Miller, 1972; Hubbs et al., 1974).

21. *Siphateles alvordensis* (Hubbs and Miller) (Alvord chub). This species inhabits creeks in the Alvord Basin of Malheur County, Oregon, and adjacent Humboldt County, Nevada. It is characterized by uniserial teeth, small, embedded scales with radii in all fields, usually seven dorsal and anal fin rays, and numerous, short gill rakers (16–22) (Hubbs and Miller, 1972).

22. *Siphateles boraxobius* (Williams and Bond) (Borax Lake chub). This small fish occurs in Borax Lake, Alvord Basin, Malheur County, Oregon. The diagnosis includes a large head, large eyes, small caudal peduncle, and a reduced lateral line. The species shares general characters with *S. alvordensis*, but it has fewer gill rakers, fewer lateral line scales, and fewer pectoral-fin rays, like many dwarf populations of *Siphateles* (Williams and Bond, 1980).

Gila–*Acrocheilus*–*Klamathella* Subgroup

23. **Gila atraria* (Girard) (Utah chub). This variable, abundant species is widespread in the Bonneville Basin and upper Snake River above Shoshone Falls. It is distinctive in its 2,5–4,2 pharyngeal teeth with grinding surfaces, 9 dorsal-fin rays, 8 anal-fin rays, and 8–16 gill rakers. It is locally divergent and polymorphic in its mtDNA. The Bear River population diverged from the Bonneville Basin populations more than 2 Ma, well before the complex Late Quaternary interactions between the Bear River and Lake Bonneville (Bouchard et al., 1998). The fossil record of *Gila atraria* is known back only to the late Pleistocene Black Rock Canyon, Smith Canyon, and Homestead Cave faunas in the Lake Bonneville drainage basin, Utah

and Nevada (Smith et al., 1968; Mead et al., 1982; Broughton, 2000a, 2000b).

24. *Gila jordani* Tanner (Pahranagat roundtail chub). This species lives in Ash Springs, Crystal Lake, and (formerly) Hiko Springs, all in Pahranagat Valley, pluvial White River system, Lincoln County, Nevada (Tanner, 1950). It has the unique combination of *Gila robusta* morphology and *G. cypha* and *G. atraria* mtDNA (Table 2); this unique combination is diagnostic for the species. *Gila jordani* is sympatric with *Lepidomeda altivelis*, *Rhinichthys osculus*, *Catostomus clarki*, and *Crenichthys baileyi grandis* (LaRivers, 1962). It has been regarded as a subspecies of *Gila robusta*, with which it was presumably connected via the pluvial White River during the last 10 Ky (Hubbs and Miller, 1948b). The principle of individuality of distinct forms of hybrid origin, as applied to *Gila seminuda* (DeMarais et al., 1992), suggests that although *Gila jordani* has been separated for only 35 Ky, it should be recognized as a species with a unique history because of its unique combination of apomorphies.

Gila (or *Moapa*) *coriacea*, the Moapa dace, is a localized relative of *Gila robusta* (Figure 2) and *G. intermedia* that inhabits warm springs in the Moapa River, which is the former lower course of the pluvial White River channel in northern Clark County, Nevada. It is not a current member of the Great Basin fauna, but it is geographically peripheral and is a relative of *Gila jordani*. *Moapa* was named by Hubbs and Miller (1948b) who considered it to be related to *Agosia*, *Rhinichthys*, and *Gila*. According to the molecular cladogram (Figure 2), it is a member of the *Gila* clade. A Pliocene or Pleistocene fossil opercle of the *Gila* group was collected by G.R. Smith from sediments exposed in a roadcut near the town of Moapa, Nevada.

25. **Klamathella* sp. (chub). *Klamathella* fossils are found in Pliocene sediments at Honey Lake, Madeline Plains, and Alturus, California. The fossils are diagnosed by their *Gila*-like pharyngeal bones with two rows of pharyngeal teeth. Fossils from the Salt Lake group (~6 Ma) at Junction Hills, Box Elder County, Utah, were reported by McClellan (1977); they are similar to fossil *Klamathella* from the Snake River Plain. *Klamathella* was formerly a subgenus of *Gila*, which was erected for *G. coerulea*. We hereby raise it to generic rank on the basis of molecular evidence that *Klamathella* and *Acrocheilus* are sister groups (Figure 2). Separation of *Klamathella* from *Gila* makes *Gila* monophyletic.

26. **Acrocheilus alutaceus* Agassiz and Pickering (chiselmouth). This is a Snake River and Columbia River species that also lives in the Harney–Malheur Basin. The basin was cut off from the Malheur River, a tributary to the Snake, by rather young volcanics (less than 1 Ma, Luedke and Smith, 1982). McClellan (1977) found *Acrocheilus* teeth in sediments of the Salt Lake group in the Junction Hills, Box Elder County, Utah. Fossils reported as *Acrocheilus* from the Madeline Plains in northeastern California (Wagner et al., 1997) may be highly variable *Lavinia*.

In the molecular phylogeny (Figure 2), *Acrocheilus* is the sister of *Klamathella coerulea*, and together they are sister to the *Gila* clade. *Acrocheilus* and *Klamathella* differ by 6.4% in their cytochrome *b* sequence (Table 2); fossils show that the apomorphic jaw-shape of *Acrocheilus* was well established on the Snake River Plain 7 Ma (Smith et al., 1982), indicating divergence from *Klamathella* (plesiomorphic) occurred prior to that date.

27. †*Gila turneri* (Eastman) (chub). This fossil form is known from the Miocene Esmeralda Formation of south-central Nevada. Specimens are also known from slightly older (~12 Ma) lacustrine beds of Stewart Valley, Mineral County, Nevada. It is characterized by a slender caudal peduncle and 10 anal-fin rays. *Gila turneri* was assigned to *Richardsonius* by LaRivers (1962), but, based upon the large anal fin, it could be related to Colorado River *Gila*, which differ from other *Gila* by an average of about 6% sequence divergence.

28. †*Gila*(?) *esmeralda* LaRivers (chub). This species from the Miocene (~12 Ma) Esmeralda Formation may be related to *Siphateles*. It has 8 anal-fin rays, the dorsal fin in advance of the pelvis, and a deep caudal peduncle (Lugaski, 1977, 1979; Smith and Miller, 1985). *Gila* and *Siphateles* differ by an average of about 11% sequence divergence (Table 2).

29. †*Gila*(?) sp. (chub). A large chub, greater than 40 cm long, with 8 anal-fin rays, 9 pelvic-fin rays, long dentaries, and blunt, slightly hooked pharyngeal teeth with no grinding surface was collected by Michael Bell from the Truckee Formation southeast of Ferndale, Nevada, in the Hemphillian Quarry (N81) along with numerous sticklebacks (~6 Ma). A similar fish was collected nearby by J. Platt Bradbury from the Eagle-Picher Mine in the Clarendonian section (~12 Ma) of the Truckee Formation (Axelrod, 1956). The Bell specimen has dentaries like those of *Gila* or *Siphateles*, but it has extremely short articular angulars, like those of *Ptychocheilus* or *Mylopharodon*. These forms could be related to *Siphateles* from Mono Lake and could be near the stem group for *Gila*, *Ptychocheilus*, *Siphateles*, and *Mylopharodon*, judging from the shape of the angulars and the dentaries. *Siphateles*, *Mylopharodon*, *Ptychocheilus*, and most *Gila* differ from each other by an average of about 10%–12% sequence divergence.

Ptychocheilus–*Relictus*–*Eremichthys* Subgroup

This group is not monophyletic in the analysis from which Figure 2 was drawn, because *Ptychocheilus* is polyphyletic in that tree. The possibility that *Ptychocheilus* is paraphyletic is supported by the existence of fossils from 15 Ma bearing *Ptychocheilus* apomorphies (Smith et al., 2000), but the issue is in need of further study.

30. **Ptychocheilus oregonensis* (Richardson) (northern pike-minnow). This Snake River–Columbia River species also lives in the Harney–Malheur Basin. *Ptychocheilus* occurred in the Pliocene Mono Basin, Alturus Basin, Madeline Plains, and Secret Valley, California (Wagner et al., 1997). It is known from Miocene (15 to ~6 Ma) and Pliocene (5.5 to 3 Ma) deposits in

the Columbia River and Snake River basins (Smith et al., 1982; Smith et al., 2000). Numerous Miocene to Pliocene sites in Carson Valley, Douglas County, Nevada (Kelly, 1994), have yielded *Ptychocheilus* dentaries, quadrates, vertebrae, a tooth, and a neurocranium. During this study a single vertebra was identified from Miocene deposits in Brady Park, Churchill County, Nevada. McClellan (1977) identified long, slender, caniniform pharyngeal teeth from the Miocene Salt Lake group in the Junction Hills, Box Elder County, Utah, as *Ptychocheilus*. Living *Ptychocheilus oregonensis* differ from their cladistic relatives by an average of 11.2% (s.d. = 2.1%) sequence divergence (Figure 14; Table 2). The oldest known fossil *Ptychocheilus* bears a well-constrained date of 15 Ma from the Columbia Basin (Smith et al., 2000).

31. *Relictus solitarius* Hubbs and Miller (relict dace). This small fish is endemic to Ruby and Butte Valleys (pluvial lakes Franklin and Gale) and to Goshute and Steptoe Valleys (pluvial lakes Waring and Steptoe); each of the four valleys compose parts of both Elko and White Pine Counties, Nevada (Hubbs and Miller, 1972). *Relictus* displays the western spring morphotype: small size (usually less than 10 cm SL), small rounded fins, no barbels, reduced lateral line, and scales not in orderly rows. It also has distinctive, cone-like nuptial tubercles on the head and pectoral fins (Hubbs and Miller, 1972). According to mtDNA evidence, it may be cladistically, but distantly related to *Eremichthys* (sequence divergence = ~15%), but its sequence is phenetically more similar to *Gila robusta* (sequence divergence = ~11%) (Table 2). The data indicate that it is an ancient relict (Figure 2), as concluded by Hubbs and Miller (1972).

32. *Eremichthys acros* Hubbs and Miller (desert dace). This is a highly localized endemic of Soldier Meadows, in the northwestern part of the Lahontan Basin. It is diagnosed by its small size (usually less than 6 cm SL), laterally broad pharyngeal arches, uniserial teeth, and specialized sheaths on the jaws (Hubbs and Miller, 1948b). According to parsimony cladistic analysis of mtDNA data, its closest relatives are *Relictus* (sequence divergence = 15%) and *Ptychocheilus* (sequence divergence = 14%), but it also shares 13% similarity with several species of *Gila*. These data indicate that it is an ancient relict, as suggested by Hubbs and Miller (1948b).

Snyderichthys–*Lepidomeda* Group

33. *Lepidomeda albivallis* Miller and Hubbs (White River spinedace). This species was found in springs and their effluents in the upper White River valley of White Pine and Nye Counties, Nevada (Hubbs and Miller, 1960), but it is now extinct. It differs from its sister species, *Lepidomeda altivelis* and *L. mollispinis*, from elsewhere in the Virgin–White drainage, by 0.5 % sequence divergence (Table 2). It lived with *Rhinichthys osculus*, *Catostomus clarki*, and *Crenichthys baileyi*.

34. *Lepidomeda altivelis* Miller and Hubbs (Pahranagat spinedace). This localized species, now extinct, lived in the Ash Spring and Pahranagat Lake area of the White River val-

ley, in Lincoln County, Nevada (Hubbs and Miller, 1960). It differed from its sister species, *Lepidomeda albivallis*, by having (on average) a more oblique mouth, a sharp snout, less dark pigment, and a larger and more pointed dorsal fin with a stronger spine.

35. *Snyderichthys copei* (Jordan and Gilbert) (leatherside chub). This apparently paraphyletic species is endemic to the Bonneville Basin, upper Snake River, and Little Wood River drainages in Utah, Wyoming, and Idaho. Its generic affinities have been ambiguous (Miller, 1945a), but Hubbs and Miller (1960) suggested a relationship to *Lepidomeda*. *Snyderichthys* shares mtDNA similarity at the level of 5% sequence divergence with the Virgin River *Lepidomeda*, which provides an important clue to its relationships and to western biogeography. *Snyderichthys* and the Virgin River and White River *Lepidomeda* spp. differ from *Lepidomeda vittata* of the Little Colorado River and from more plesiomorphic members of the plagiopeterin clade (Simons and Mayden, 1997; Dowling et al., 2002) by 8%–9% sequence divergence (Figure 2; Table 2). This pattern of relative similarity in mtDNA indicates the relationships among the northern and southern members of this species are complex (Dowling et al., 2002). The Bear River and Snake River populations are more similar to Virgin River drainage *Lepidomeda* (5% sequence divergence) than to Sevier River and other Bonneville Basin *Snyderichthys* (11%–12% sequence divergence; Table 2), suggesting there has been independent loss of spines or introgressive transfer of mtDNA in *Snyderichthys*. This pattern of mtDNA similarity supports other evidence for a former drainage connection between the upper Snake River and the Virgin–White drainage of the Mio–Pliocene Bouse Embayment (see “Discussion”). Additional evidence of this connection is the presence of the Muddy Creek Formation from the Lake Mead area to the southwestern Escalante Desert of the Bonneville Basin, prior to 4 Ma (Spencer Reber, pers. comm. to G.R.S., 1999).

Iotichthys–*Richardsonius*–*Rhinichthys*–*Mylocheilus* Group

36. *Iotichthys phlegthontis* (Cope) (least chub). This small species is endemic to the Bonneville Basin. It was formerly known from eastern tributaries to the Great Salt Lake south to Snake Valley and Juab County, Utah. It shares a unique morphological character, namely retarded closure of the posterior cranial fontanel by the parietal, with *Gila atraria* (Coburn and Cavender, 1992:346), but it shares its mtDNA haplotype with *Richardsonius* (sequence divergence 9% with *R. balteatus*; 18% with *G. atraria*) (Figure 2; Table 2). Incongruent morphological and molecular characters suggest there has been introgressive transfer of either morphology or mtDNA from either *Gila atraria* or *Richardsonius* (respectively) to *Iotichthys* (Figure 2 versus Figure 3).

37. **Richardsonius balteatus balteatus* (Richardson) (Columbia reddsider). This subspecies is characterized by its long anal fin. It lives in the Columbia River drainage and in the Great Basin. In the latter, it inhabits the Silvies River of the

Harney–Malheur Basin (Bisson and Bond, 1971). We infer that it dispersed north from the Columbia Basin postglacially because it is not in northern refugia. Although *Richardsonius* is a solely western North American genus, it is closest to eastern North American *Clinostomus* (sequence divergence = 12%; Dowling, unpublished data). There is a fossil record of the *R. balteatus* lineage from the Pliocene (~3.5 Ma) of the Snake River Plain (Smith et al., 1982).

38. **Richardsonius balteatus hydrophlox* (Cope) (Bonneville reidside shiner). This subspecies differs from *R. b. balteatus* in having fewer anal-fin rays. It is found in the Bonneville Basin, in isolated creeks of the Harney–Malheur Basin, and above barrier falls in the Snake River drainage and in the South Fork of the John Day River in Oregon (Bisson and Bond, 1971). The presence of relicts of this subspecies above various barrier falls in the Columbia River drainage suggests that the plesiomorphic morphology of this subspecies represents an earlier form than its sister subspecies, *R. b. balteatus*. It presumably dispersed after connection of the Snake River to the Columbia River about 2 Ma, but before formation of the falls and other causes of isolation in the late Pleistocene. A fossil right pharyngeal arch of *R. balteatus*, presumably *R. b. hydrophlox*, was recovered by G.R.S. from Wisconsin deposits in Homestead Cave, northern Bonneville Basin (Broughton, 2000a).

39. *Richardsonius egregius* (Girard) (Lahontan redside). This small shiner and its cohabitant in the Lahontan Basin, *Catostomus tahoensis*, are the only widespread endemic species of the Great Basin. Their absence from surrounding basins is (weak) evidence against low-elevation drainage connections between the Lahontan Basin and other basins in the last several million years. *Richardsonius egregius* is abundant in diverse habitats, but it has not differentiated as much as *Siphates* or *Rhinichthys*. It differs from its sister species, *R. balteatus*, primarily in its smaller body size and smaller fins.

40. *Rhinichthys cataractae* (Valenciennes) (longnose dace). This one of the most widely distributed fishes in North America, especially in the eastern and northern parts of the continent. Within the Great Basin, it is found in the northeastern Bonneville Basin, specifically the Provo River, and northward into Utah, Idaho, Wyoming, and the Harney–Malheur Basin of Oregon.

Rhinichthys (Apocope) osculus (Girard) (speckled dace). This is a ubiquitous, polytypic species in the Great Basin and surrounding waters; its subspecies are summarized in the entries to follow. Geographic and ecophenotypic variation is extreme in Great Basin representatives of this species (Hubbs et al., 1974). The general pattern of variation usually trends toward one of two ecological morphotypes. The lotic morphotype has a well-developed frenum and barbels, 2,4–4,2 pharyngeal teeth, small scales, medium-sized fins, and a fusiform body shape that is adapted to rheophilic life. The lentic morphotype is a reductively evolved form; it has a reduced frenum, barbels, and lateral line; 1,4–4,1 teeth; small, rounded fins; small body size; and inhabits quiet, isolated waters

(Hubbs et al., 1974; Miller, 1984:15). The following subspecies represent only part of the variation in the group.

41. *Rhinichthys osculus carringtoni* (Cope) (Bonneville speckled dace). This subspecies name applies not only to Bonneville Basin, upper Snake River, and most Harney–Malheur Basin populations, but also to the lower Snake River and some Columbia Basin populations. This morphotype is probably an early form of the genus. The features of the lotic morphotype, listed above, characterize *R. o. carringtoni*; however, the Harney–Malheur Basin fish are smaller and have reduced barbels, especially in Warm Springs (Bisson and Bond, 1971). Hubbs and Miller (1948b) suggested that the Warner Basin contains three subspecies of *R. osculus*.

42. *Rhinichthys osculus adobe* (Jordan and Evermann) (Sevier speckled dace). This dace of the southern Bonneville Basin is distinctive in its large head, large, horizontal mouth, flat snout, and many pigment differences (Hubbs et al., 1974).

43. *Rhinichthys osculus velifer* Gilbert (Pahranagat terete dace). This dace inhabits the swift water outflow of Ash Springs, in Pahranagat Valley, Lincoln County, Nevada. The fish is slender, with barbels, a frenum, and large, falcate fins (Miller, 1984:15,17–18).

44. *Rhinichthys osculus robustus* Rutter (western speckled dace). This name was applied to the form of *Rhinichthys osculus* of the Sacramento River, Lahontan Basin, and some associated drainages by Snyder (1917a) and Hubbs et al. (1974). It is characterized by possession of barbels and usually 1,4–4,1 pharyngeal teeth. Prior to 3.2 Ma, the Sacramento and Lahontan drainages were connected by a pass at the head of San Joaquin Canyon in Mono and Madera Counties, California (G.I. Smith, pers. comm. to G.R.S.). The form in Soldier Meadows, Humboldt County, Nevada, shows possible evidence of introgression—it usually has the normal tooth formula of 1,4–4,1, but a unique specimen has 0,5–4,0, like sympatric *Eremichthys acros* (Hubbs and Miller, 1948a:17).

45. *Rhinichthys osculus nevadensis* (Gilbert) (Amargosa speckled dace). This fish lives in Ash Meadows, Nye County, Nevada. It is small, with barbels, large scales, an incomplete lateral line, 1,4–4,1 teeth, and no frenum. Its closest relative was *Rhinichthys osculus deaconi* (Las Vegas dace), which was endemic to Las Vegas Creek and Las Vegas Springs, which were tributary to the Colorado River (Hubbs and Miller, 1948a; Miller, 1984). The Amargosa and Las Vegas drainages are connected by the Indian Springs Basin, a large section of which was captured by, and is now a tributary to, the Amargosa River (Gilluly, 1929:682; Miller, 1946a). The similarity of the subspecies *R. o. deaconi* and *R. o. nevadensis* indicates a confluence of fish habitat and gene flow occurred between the Las Vegas and Indian Springs Valleys, probably in the pass occupied by the old railroad bed and Highway 95 east of Indian Springs.

46. *Rhinichthys osculus deaconi* Miller (Las Vegas speckled dace). This subspecies (now extinct) was endemic to Las Vegas Creek and Las Vegas Springs, which were tributary to the

Colorado River in pluvial times. It was characterized by a uniquely rounded anal fin, large scales, small pectoral fins, 1,4–4,1 teeth, no barbel or frenum, and an incomplete lateral line (Miller, 1984).

47. *Rhinichthys osculus reliquus* Hubbs and Miller (Grass Valley speckled dace). This form lived in the valley of pluvial Lake Gilbert, Lander County, Nevada, and is probably extinct. It lacked barbels and had a much-reduced lateral line (Miller, 1984).

48. *Rhinichthys osculus oligoporus* Hubbs and Miller (Clover Valley speckled dace). Clover Valley is in the valley of pluvial Lake Clover, Elko County, Nevada. *Rhinichthys osculus oligoporus* lacks barbels and has a reduced lateral line (Miller, 1984).

49. *Rhinichthys osculus lethoporus* Hubbs and Miller (Independence Valley speckled dace). This subspecies lives in Independence Valley, a tributary to the valley of pluvial Lake Clover, Elko County, Nevada. It was apparently derived from *R. o. robustus* of the Lahontan Basin drainage (Hubbs et al., 1974). It is small and compressed, lacks a frenum and barbels, and has a reduced lateral line.

50. *Rhinichthys osculus lariversi* Lugaski (Big Smokey speckled dace). Described as a new species by Lugaski (1972), this form was regarded as a subspecies by Hubbs et al. (1974) and Miller (1984). It lives in the valley of pluvial Lake Toiyabe in Lander and Nye Counties, Nevada. This fish has 62–70 lateral scale rows, 1,4–4,1 pharyngeal teeth, 8 dorsal-fin rays, 7 anal-fin rays, no frenum, and variable development of barbels and lateral line. The Lahontan form of *R. o. robustus* is its closest relative; Hubbs and Miller (1948b) hypothesized that *R. o. lariversi* gained access to the valley of Lake Toiyabe through a stream connection with the valley of Lake Gilbert, on its northern border. The taxon is unusual in that it coinhabits the springs on the east side of the valley with a local form of *Siphateles bicolor obesus*. In most areas of the western Great Basin only a single form of *Rhinichthys* or *Siphateles* exists in a given spring, or *Siphateles* lives in the spring and *Rhinichthys* lives below the spring outflow.

51. *Rhinichthys osculus moapae* (Williams) (Moapa dace). This subspecies was described from the Moapa River, Clark County, Nevada. It is a rheophile and has barbels, a frenum, falcate fins, and silver coloration (Williams, 1978).

52. *Rhinichthys osculus* subsp. (Meadow Valley Wash dace). This inhabitant of springs in Lincoln County, Nevada, is a large dace with small scales, a complete lateral line, a frenum, barbels, 1,4–4,1 pharyngeal teeth, and 37–39 vertebrae (Miller, 1984).

53. *Rhinichthys osculus* subsp. (Pahranagat speckled dace). The subspecies occurs in Lincoln and Clark Counties, Nevada. It has rather large scales, small fins, an incomplete lateral line, and reduced number and size of barbels, but it has 2,4–4,2 pharyngeal teeth (Miller, 1984).

54. *Rhinichthys osculus* subsp. (White River shortfin dace). The dace that lives in quiet waters of the White River

valley in White Pine County, Nevada, is an undescribed subspecies with robust body, small rounded fins, no barbels, no frenum, and 2,4–4,2 pharyngeal teeth (Miller, 1984).

55. *Rhinichthys* sp. (Deep Creek dace). This endemic species has been collected in the western Bonneville Basin, from Fish Springs to Snake Valley. It differs from other robust *Rhinichthys osculus* in color, body shape, meristics, and 2,4–4,2 pharyngeal teeth (R.R. Miller and G.R. Smith, unpublished data).

56. †*Mylocheilus inflexus* (Cope) (Chalk Hills chub). This fossil form of *Mylocheilus* from Idaho and Nevada is similar to *Mylopharodon* (Appendix, number 5) in the possession of molariform teeth. The two lineages may have hybridized in the past, according to molecular and fossil evidence (Dowling and Smith, unpublished data). Mitochondrial DNA data indicate that *Mylocheilus caurinus* (number 58 in Table 2) belongs in the shiner clade with *Richardsonius* (sequence divergence = 33%, Table 2). Miocene(?) chub pharyngeals from Brady Pocket (Churchill County, Nevada, collected by Charles Dailey) are similar to specimens of *M. inflexus* from the late Miocene (~7 Ma) Snake River Plain (Smith et al., 1982, fig. 4A). This suggests a Miocene connection existed between central Nevada and the Snake River Plain.

57. †*Mylocheilus* sp. (chub). A pharyngeal arch and teeth of a *Mylocheilus*, intermediate between *M. inflexus* and *M. robustus*, were collected from the Salt Lake group at Junction Hills, Box Elder County, Utah (McClellan, 1977). Correlation with other *Mylocheilus* suggests that the Junction Hills fauna is Hemphillian in age. The presence of this form and fossil *Ameiurus* in the fauna agrees with molluscan evidence for a Miocene connection and subsequent isolation between waters in northern Utah and the western Snake River Plain (Taylor, 1966).

58. †*Mylocheilus robustus* (Cope) (baby-jaw chub). This species was described from late Miocene and Pliocene pharyngeal arches from the Snake River Plain; the arches are large and have molar teeth. Similar arches with molariform teeth are in beds dated from the late Clarendonian to Hemphillian in the Virgin Valley Formation, Nevada. A single tooth fragment from the Barstovian to Hemphillian age in Esmeralda Formation equivalent beds of Stewart Valley, Nevada, may represent this species (but see *Mylopharodon* from the Esmeralda Formation). *Mylocheilus robustus* is replaced in the modern Snake River and Columbia River drainages by *Mylocheilus caurinus*.

CATOSTOMIDAE

59. †*Deltistes* sp. (Fort Rock Lake sucker). Rare maxillae and dentaries from Pliocene localities at Fossil Lake, Fort Rock Basin, Oregon, have characters that separate these fish from the abundant *Chasmistes* in the basin. The maxilla has a posteriorly directed premaxillary process and a general shape similar to *Deltistes luxatus* of Klamath Lakes basin. The ventral keel of the maxilla is prominent anteriorly; the dorsal keel is weak,

with a long convex slope anteriorly. The dentaries are shorter and more robust than those of the *Chasmistes* clade, with the gnathal ramus deflected mesially and lacking a ventral concavity. An almost complete Weberian apparatus, similar to that of the *Deltistes* clade of the Snake River Plain, was collected by Sue Ann Bilby from sediments of the Salt Lake group, near Georgetown, Idaho.

60. **Chasmistes cujus* Cope (cui-ui). This is a large planktivore in Pyramid Lake that formerly occupied Lake Lahontan and its postpluvial remnants. It has the most specialized morphology among the Holocene species in the genus. Fossil dentaries, vomer, pterotic, and vertebrae from sediments of the Humboldt River canyon confirm the presence of *Chasmistes* in the pre-Lahontan system in the middle Pleistocene. Pleistocene fossils were collected from near Fallon, Nevada, by J.R. Alcorn. A similar form is found in Pliocene sediments at Secret Valley and Honey Lake, California (see below; Taylor and Smith, 1981). *Chasmistes cujus* is known from widespread Lahontan Basin Indian middens, such as those in Humboldt Cave, Lovelock Cave, Fishbone Cave, and Hidden Cave, Nevada, and in Karlo, California (Hubbs and Miller, 1948b:41; Follett, 1963, 1967, 1980; Miller and Smith, 1981; Smith, 1985). These specimens were probably transported by American Indians from Pyramid and Walker Lakes.

61. **Chasmistes liorus* Jordan (June sucker). This species is now endemic to Utah Lake, but it was probably a Pleistocene inhabitant of Lake Bonneville. It is apparently not closely related to *Chasmistes muriei*, the form that survived in the upper Snake River (Miller and Smith, 1981). *Chasmistes* that were not diagnostic to species were collected from the Thatcher Basin near Preston in southeastern Idaho by R.C. Bright (1967). *Chasmistes* fossils were collected by McClellan (1977) from sediments of the Salt Lake group at Junction Hills, Box Elder County, Utah.

Chasmistes muriei of Jackson Hole, Wyoming, was native to the upper Snake River drainage, where one specimen was collected in the 1930s, but it is now apparently extinct. The morphology of *C. muriei* is similar to that of *C. batrachops* (extinct, Fossil Lake) or *C. brevirostris* (Klamath drainage). Pliocene fossils from the Teewinot Formation, upper Snake River drainage in Teton County, Wyoming, are similar to *C. muriei* in the Snake River and to *C. brevirostris* in the Klamath Basin (Miller and Smith, 1981).

62. †*Chasmistes batrachops* Cope (Fossil Lake sucker). This sucker was described from Pliocene or Pleistocene sediments of Fossil Lake, Fort Rock Basin, Oregon. Its dentary and maxillary osteology is generalized. The name may be applicable to similarly generalized bones from the Pliocene Glens Ferry Formation of Owyhee County, Idaho (not *Chasmistes spatulifer*); Mono Basin, Mono County, California; China Lake and White Hills, Inyo County, California; and Duck Valley, Washoe County, Nevada (Miller and Smith, 1981). *Chasmistes* bones are variable in Fossil Lake, perhaps

because Pliocene and Pleistocene remains might be mixed as lag clasts on deflation surfaces in the basin.

63. †*Chasmistes* sp. indeterminant (Mono Basin lake sucker). This lake sucker is found in Pliocene sediments of the Mono Basin, California, with *Ptychocheilus*, *Siphateles*, *Catostomus*, and Pliocene mollusks (Taylor, 1966). Skulls from Mono Basin resemble skull bones of *C. batrachops* from Fossil Lake, Oregon. Dentaries and maxillae from Mono Basin are similar to those from Secret Valley, California. Dentaries are similar to those of *C. batrachops* from Fossil Lake (UMMP 74488) in the medially flattened ridge, in the depth of the groove between the gnathal ridges, and in the anterior recess caudal to the symphysis and gnathal ridges. The position of the median mental foramen and the end of the Meckelian groove are similar to those of *C. batrachops* from the Snake River Plain (UMMP 72458). Maxillae are similar to those from Fossil Lake (UMMP 774490) in the narrow, pointed dorsal keel.

64. †*Chasmistes* sp. (Carson Valley lake sucker). An early Blancan form from Carson Valley, Douglas County, Nevada, is known from dentaries and a maxilla; late Blancan fossils include an opercle, dentaries, and a vomer; an Irvingtonian dentary extends the record into the Pleistocene. The axial ridge of the vomer is broad and flat, as in *Chasmistes* and *Xyrauchen*, but lacks the postrostral constriction of *Catostomus*. The dentaries are more slender than those of *Catostomus* but are similar to those of *Chasmistes*. The medial ridge posterior to the symphysis resembles that of *C. batrachops*, but it is less pronounced than those of the Mono and Lahontan Basins and those of *C. spatulifer* of the Snake River Plain.

65. †*Chasmistes* sp. (Honey Lake sucker). This species was collected from Pliocene sediments of "The Island" of Honey Lake by Taylor and Smith (1981) and Charles Dailey. The Honey Lake sucker is intermediate between *C. cujus* of the Lahontan Basin system and *C. spatulifer* of the Snake River Plain (Miller and Smith, 1981). It is found with *Oncorhynchus* cf. †*lacustris*, *Gila*, *Siphateles*, and *Catostomus*. Similar bones are known from Duck Valley, Washoe County, Nevada, and from the Alturus Basin, the Madeline Plains, and Secret Valley of northeastern California.

66. **Catostomus ardens* Jordan and Gilbert (Utah sucker). This species is native to the Bonneville Basin drainage in Utah and to the upper Snake River drainage in Utah, Idaho, and Wyoming. It is an old lineage that is related to *Catostomus macrocheilus* of the lower Columbia drainage and to *Catostomus latipinnis* of the Colorado River drainage (Smith, 1992b; Figure 5). During the drought in the early 1930s, *Catostomus ardens* hybridized with *Chasmistes liorus* on spawning grounds in the Provo River, Utah, resulting in introgression that is still seen in *Chasmistes liorus* specimens (Miller and Smith, 1981). Late Pleistocene fossils were reported from the Hot Springs locality, Salt Lake County, Utah (Smith et al., 1968); from Homestead Cave, Tooele County, Utah (Broughton, 2000a), and from the Old River Bed between northern Bonneville and Sevier Basins, Millard County, Utah (Oviatt, 1984). A small,

nearly complete Weberian apparatus, similar to that of *Catostomus ardens*, was collected from sediments of the Salt Lake group near Georgetown, Idaho, by Sue Ann Bilby and has been deposited in the Idaho State Museum of Natural History.

67. **Catostomus macrocheilus* Girard (largescale sucker). This Holocene species was a lower Columbia River (Ringold Formation) sucker in the Pliocene; fossil evidence indicates that it spread to the Snake River basin in the late Pliocene (~2.8 Ma), after capture of the Snake River at Hell's Canyon (Smith et al., 2000). It spread north of the Columbia as the glaciers receded. It persists in the Harney–Malheur Basin as a relict of the former Snake River outlet through Crane Gap or Malheur Gap. Fossil ages indicate that the colonization of the Harney–Malheur Basin could have occurred after the species immigrated south through Hell's Canyon and prior to (or even after, until about 9 Ka) occlusion of the outlet to the South Fork of the Malheur River by the Voltage lava flow (Piper et al., 1939), 0.04–1 Ma (Gehr and Newman, 1978; Luedke and Smith, 1982).

68. †*Catostomus cristatus* Cope (sucker). This fossil species is best known from the Pliocene of the Snake River Plain. A complete maxilla was collected by Charles Dailey in deformed Pliocene sediments on "The Island" of Honey Lake. The species is diagnosed by the slender anterior neck of the maxilla in the vicinity of the ventral maxillary muscle, anterior to the dorsal and ventral crests (Taylor and Smith, 1981, pl. 19: fig. 3) and the long, gently curved gnathal ramus of the dentary (Taylor and Smith, 1981, pl. 19: figs. 5, 6).

69. †*Catostomus* sp. (Secret Valley sucker). This form displays characters of *C. cristatus* (Pliocene) and *C. macrocheilus* (Holocene) of the Snake and Columbia Basins, respectively. As in *C. macrocheilus*, the dentaries are short, relatively straight, and wide anteriorly, with strong ridges for the labial cartilage (Smith, 1975, fig. 12I). The maxillae have medium-high dorsal and ventral ridges and a general shape like those of the Wall Canyon *Catostomus*; however, the ridge for insertion of the palatine ligament (the anterior edge of the bone), although mostly vertical, has a small, horizontal, J-shaped curve that resembles the condition in *C. shoshonensis* (Smith, 1975, fig. 12A and points *xpy* on fig. 12G). McClellan (1977) collected similar sucker bones from the Salt Lake group at the Junction Hills, Box Elder County, Utah. Suckers from the Alturus Formation may be correlated with the Secret Valley form (Wagner et al., 1997). Age of the Alturus beds is correlated with the Pliocene Glens Ferry Formation by a tephra at Crowder Flat Road near Alturus, California, which bears the chemical signature of a Pliocene ash of the Glens Ferry Formation (Swirydczuk et al., 1982).

70. †**Catostomus shoshonensis* Cope (Shoshone sucker). This species (including its synonym, *C. ellipticus*) is from the Miocene and Pliocene Snake River Plain (Smith et al., 1982) and from Pliocene sediments at Honey Lake, California (Taylor and Smith, 1981). *Catostomus shoshonensis* is diagnosed by an elliptical maxilla with the attachment of the pa-

latine ligament high on the neck of the anterodorsal process (Smith, 1975, fig. 12A). This form is represented by the relict sucker of Wall Canyon, Surprise Valley, Nevada; this conclusion is based upon the shape of the maxilla.

71. *Catostomus warnerensis* Snyder (Warner sucker). This species lives in the Warner Valley in eastern Lake County, Oregon, and is similar to *Catostomus shoshonensis* of the Snake River Plain. It is also osteologically similar to the form in Wall Canyon, Surprise Valley, Nevada.

72. **Catostomus tahoensis* Gill and Jordan (Tahoe sucker). This Holocene sucker lives only in the Lahontan Basin. Fossils have been found in Pliocene sediments at Mopung Hills, Churchill County, Nevada (Taylor and Smith, 1981), in middle Pleistocene, pre-Lahontan sediments of the Humboldt River canyon, and in Holocene Indian midden material in the western part of the Lahontan Basin (Thomas, 1985:172, and references therein). The maxilla has a thick anterior segment in the vicinity of the ventral maxillary muscle attachment, with low dorsal and ventral keels that are similar to maxillae of *Pantosteus* (mountain suckers). The dentary has a mesially inflected gnathal ramus suggestive of the plesiomorphic mountain suckers. *Catostomus tahoensis* was a basal member of the *Pantosteus* clade in the cladogram of Smith and Koehn (1971). This is supported by the maxillary shape of Holocene and fossil maxillae, which are *Pantosteus*-like (Taylor and Smith, 1981, pl. 19: 1, 2). Additional material representing *C. tahoensis* was collected by Marith Reheis (USGS) from sediments deposited ~1 Ma at Sunshine Amphitheater (northwest of Walker Lake) and Lone Tree Mine, Nevada, and by J.R. Alcorn from near Fallon, Nevada.

73. **Catostomus fumeiventris* Miller (Owens sucker). This species is osteologically similar to *C. tahoensis*, except in details described by Miller (1973). It is less derived than the Mopung Hills form of *C. tahoensis*. Fragments of *Catostomus fumeiventris*(?) were recovered from the Pleistocene Owens Lake core (Firby et al., 1997). Holocene Indian midden materials from along the Owens River near the Alabama Hills in Inyo County, California, are rich in remains of the Owens sucker and *Siphateles bicolor snyderi*.

74. †*Catostomus* sp. (Mono Basin sucker). This Pliocene fish lived with *Chasmistes* sp., *Ptychocheilus* sp., and *Siphateles* sp. Its dentary has an abrupt anterior edge of the coronoid process, which is similar to that of *Catostomus fumeiventris* of Owens Valley (Miller, 1973) and to *C. tahoensis* (see Reheis et al., 2002). The maxilla is similar to that of *Catostomus cristatus* of the Miocene and Pliocene Snake River Plain, Idaho (Smith, 1975, fig. 12G), and Secret Valley, California.

75. †*Catostomus* sp. (Carson Valley sucker). Pliocene sediments in Carson Valley contain remains of a *Catostomus* associated with *Siphateles*, *Ptychocheilus*, *Lavinia*, *Chasmistes*, and *Oncorhynchus*. The dentary of this form is more similar to *C. occidentalis* than to *C. tahoensis* or *C. fumeiventris* in the weak peripheral labial ridge and the modest scalloping of the lateral surface of the precoronoid ramus. These characters sug-

gest a pre-Lahontan connection existed that allowed populations of *C. occidentalis* of the Sacramento River drainage to mix with the Carson Valley sucker of the pre-Lahontan drainage. According to G.I. Smith (pers. comm. to G.R.S., 1999), such a connection existed at the head of the San Joaquin Canyon prior to being blocked by volcanics 3.2 Ma.

76. **Catostomus columbianus* (Eigenmann and Eigenmann) (bridgelip sucker). This species of mountain sucker (subgenus *Pantosteus*) is native to the Columbia Basin and further north, but within the Great Basin it is restricted to the Harney–Malheur Basin. It normally has small scales, but in the Harney–Malheur Basin it has large scales and similarities to isolated headwater populations found in the Columbia–Snake Basin (Smith, 1966; Bisson and Bond, 1971). *Catostomus columbianus* is represented in the Pliocene of the Snake River Plain. Miller and Smith (1981) described the Pliocene specimens as a new species, *C. arenatus*, but, because no evidence of lineage splitting has been found, there is no need for the fossil name.

77. *Catostomus discobolus* Cope (bluehead sucker). This species of mountain sucker (subgenus *Pantosteus*) arose in the upper Colorado River drainage, but it is also native to the Weber River, Bear River, and upper Snake River drainages (Figure 7; Smith, 1966). It is the sister species to *C. clarki* of the lower Colorado River drainage; the two species are the most morphologically apomorphic in the genus. *Catostomus discobolus* is the most widespread mountain sucker in the upper Colorado River drainage, indicating this was the area of its origination and subsequent dispersion. Populations spread from the headwaters of the Green River to the headwaters of the Bear River via stream capture at the east end of the Uinta Mountains, perhaps before the upper Bear River was diverted from the Snake River to Lake Bonneville (Bright, 1967; Bouchard et al., 1998). It is reported from Pleistocene deposits in Homestead Cave near Great Salt Lake by Broughton (2000a). Stream capture in the headwaters of Chalk Creek, Summit County, Utah (Hansen, 1969) could have transferred *C. discobolus* from the Bear River to the Weber River.

78. *Catostomus clarki* (Baird and Girard) (desert sucker). This sister species to *C. discobolus* occupies headwaters of the lower Colorado River drainage below the Grand Canyon. It inhabits Great Basin streams that were formerly connected to the Colorado River in the Pahrnagat Valley–White River drainages in eastern Nevada and co-occurs with species of clades *Lepidomeda*, *Rhinichthys*, and *Crenichthys*. It is clinally variable in the Virgin River drainage. Northern populations possess high scale counts similar to those of *C. platyrhynchus* in the adjacent southern Bonneville Basin (see “Discussion”).

79. **Catostomus platyrhynchus* (Cope) (mountain sucker). This species of the subgenus *Pantosteus* lives in the Bonneville and Lahontan drainages, but probably early in the Pleistocene it spread north to the Snake and Columbia drainages, then east to the Colorado and Missouri drainages (Smith, 1966). Pleistocene fossils are unknown from the Great Basin,

but specimens have been collected by J.D. Stewart from the Pleistocene of northwestern Nebraska. It is the sister to the clade of three species, *C. santaanae* (of the Los Angeles Basin), *C. clarki* (lower Colorado River drainage), and *C. discobolus* (upper Colorado River drainage). Differences between the Bonneville Basin and Lahontan Basin forms are slight. The population of *C. platyrhynchus* in Shoal Creek, Washington County, Utah, shows introgressed characters from *C. clarki* of the Virgin River drainage, possibly as a result of genetic contact at the time of the outlet of Lake Bonneville to Meadow Valley Wash in the middle Pleistocene (Ives, 1948).

ICTALURIDAE

80. †*Ameiurus hazenensis* Baumgartner (Truckee bullhead). This is one of only two Late Cenozoic catfishes of the Great Basin. It is known only from late Miocene sediments of the Truckee Formation, near Hazen, Nevada (Baumgartner, 1982). *Ameiurus hazenensis* is related to *A. peregrinus* of the Chalk Hills Formation, Oregon, to *A. vespertinus* of the Glenns Ferry Formation, Idaho (Lundberg, 1992), to *Ameiurus* sp. from the Junction Hills, Box Elder County, Utah (see number 81, below), and to *Ameiurus reticulatus* from the Ringold Formation of Washington (Smith et al., 2000).

81. †*Ameiurus* sp. (Junction Hills bullhead). McClellan (1977) collected spines of a small bullhead, possibly of Hemphillian age, from the Junction Hills, Box Elder County, Utah.

SALMONIDAE

COREGONINAE

82. **Prosopium williamsoni* (Girard) (mountain whitefish). This widespread western North American mountain species lives in the Bonneville, Harney, Lahontan, and surrounding basins (Figure 8). Fossil scales of *Prosopium* (not necessarily *williamsoni*) were taken from the Old River Bed units of Lake Bonneville (Oviatt, 1984) and the Pleistocene part of the Owens Lake core (Firby et al., 1997). The earliest known form of *Prosopium*, i.e., *P. prolixus*, occupied Lake Idaho on the Snake River Plain throughout much of the Pliocene (Smith, 1975). Cold adaptations, cladistic relationships, and paleogeography indicate that the genus *Prosopium* is northern in origin.

83. *Prosopium abyssicola* (Snyder) (Bear Lake whitefish). This whitefish is now endemic to Bear Lake, a part of the Bear River drainage, which is a tributary to Lake Bonneville. It is not represented among the abundant Lake Bonneville fish bones examined by Smith et al. (1968) or Broughton (2000a, 2000b).

84. **Prosopium spilonotus* (Snyder) (Bonneville whitefish). This species is now a Bear Lake endemic. *Prosopium spilonotus* existed in late Lake Bonneville (Smith et al., 1968; Broughton, 2000a, 2000b).

85. **Prosopium gemmifer* (Snyder) (Bonneville cisco). *Prosopium gemmifer* is a specialized planktivore that is now endemic to Bear Lake, but a similar form also occurred in Lake Bonneville (Smith et al., 1968; Broughton, 2000a, 2000b). The two forms of *P. gemmifer* differ significantly in bones that reflect the shape of the head and jaws. The Bear River was a tributary to the Snake River prior to the late Pleistocene diversion of the Bear River into the Bonneville Basin at Soda Springs (Bright, 1967; Bouchard et al., 1998).

THYMALLINAE

86. *Thymallus arcticus* (Pallas) (Arctic grayling). Grayling have not been previously acknowledged as native to the Great Basin fauna, but they were recognized among fishes collected in 1834 from the Bear River near Georgetown, Idaho, by John Kirk Townsend (1978:89). Townsend was a physician and zoologist working with Thomas Nuttall, a British botanist from Harvard University who was en route to the Columbia River. Nuttall was familiar with Great Lakes fauna, which includes grayling and char. Townsend was the first trained zoologist to cross the American continent, collecting specimens and recording observations of natural history. Townsend recorded grayling with trout and whitefish in the headwaters of the Green River (1978:84 (June 30)) and contrasted them in a way that implies that he and Nuttall knew the difference between grayling and whitefish: "The river, here, contains a great number of large trout, some grayling, and a small, narrow-mouthed whitefish, resembling a herring. They are all frequently taken with the hook." On the Bear River, about 12 miles south (upstream) of Soda Springs, Idaho, on 6 July 1834, Townsend (1978:89) wrote: "Trout, grayling, and a kind of char are very abundant here—the first very large." On the previous day, he recorded: "This is a fine stream of about 150 feet in width, with a moveable sandy bottom." (This was prior to the overgrazing, erosion, and destruction of these aquatic habitats that commenced three to four decades later.) Grayling are now native, nearby, to the upper Missouri River in Montana, in streams that were tributaries to the Hudson Bay during preglacial and early glacial times (Menely et al., 1957; Howard, 1960; Lemke et al., 1965:15). Grayling had access from the upper Missouri River to the North Platte River, the upper Green River basin (Sears, 1924; Bradley, 1936), the upper Snake River, the Bear River, and the Bonneville Basin through headwater-stream captures northeast of the Uinta Mountains (Hansen, 1969; see "Discussion"). There are no Holocene or fossil specimens from the Great Basin in the collections we examined.

SALMONINAE

87. **Salvelinus confluentus* (Suckley) (bull trout). Townsend (1978), in the account of his (1834) westward journeys, reported "charr" from the Bear River, as pointed out by Roslund (1951). That the upper Bear River was sufficiently cold

and stable in 1834 to support grayling, char, and large trout (Townsend, 1978:88; see *Thymallus arcticus*, above) has rarely been considered. In 1934, Steven D. Durrant, of the University of Utah, discovered a population of *S. confluentus* in the Jarbidge drainage, a tributary to the Snake River drainage, north of the edge of the Great Basin (Miller and Morton, 1952; Cavender, 1978). Hubbs and Miller (1948b) captured specimens in the Lost River system on the eastern Snake River Plain, an area that shares most of the Bonneville Basin fauna. Bull trout could have colonized the Bonneville Basin from the Snake River while Lake Bonneville was a tributary to the Snake River (Bright, 1967). *Salvelinus confluentus* might have gained access to the Snake River via headwater transfer from the Salmon River (Behnke in Cavender, 1978) and then to the Bear River when it was a tributary to the Snake River. Char also could have occupied the Great Basin throughout the late Cenozoic. One premaxilla with diagnostic characteristics of *S. confluentus* was identified by Jack Broughton from abundant fossils in Homestead Cave (Broughton, 2000a, 2000b). We (GRS and KWG) have examined the maxilla and concur in the identification; we are searching for additional bones to confirm the record. In the middle Miocene, about 14 Ma, *Salvelinus* was in central Nevada (Churchill County, collected by J.R. Alcorn and Ted Cavender; UMMP57107) and in the Columbia River drainage of Idaho (Smiley and Rember, 1985) as *Hucho* sp. (Smith and Miller, 1985). It lived in the Snake River Plain in the late Miocene (referred to as †*Hucho larsoni*) (Kimmel, 1975; Smith et al., 1982). Native *Salvelinus* are now extinct in the Great Basin.

88. †*Oncorhynchus cynoclope* (LaRivers) (Rabbit Hole trout). This trout was named for Rabbit Hole, Pershing County, Nevada, by LaRivers in 1964. "*Salmo esmeralda*" was named by LaRivers in 1966; the description was based upon fragmentary material from the late Miocene Alum Mine, Nye County, Nevada, in the upper portion of the Esmeralda Formation. It is not clear how these trouts are related to each other or to a trout from the Miocene Truckee Formation of western Nevada. The oldest name is used until more material enables more detailed comparisons. Salmonid bones from Stewart Valley, Mineral County, Nevada, are slightly older than the specimens from the Esmeralda Formation (15–12 Ma, radiometric date); they were found with plants, insects, mammals, and other fishes. A late Hemphillian salmonid dentary was collected by Tom Kelley with mammals from the Coal Valley Formation, Mineral County, Nevada. A trout from Carson Valley, Nevada, is known from vertebrae of individuals about 45 and 54 cm in standard length. The perforated pattern on the centra of the vertebrae and the smooth connections of the arches to the centra indicate the vertebrae are different from recent salmon and trout. A dentary of a similar salmonid was collected by Lily Lugaski with cyprinid bones and fossil plants from the Buffalo Canyon Formation (~15 Ma), Churchill County, Nevada.

89. †*Oncorhynchus* sp. (Truckee trout). The Truckee Formation produced a small, nearly complete trout collected by

Michael Bell from a diatomite mine near Hazen, Nevada. The late Miocene diatomite deposit also produced *Fundulus*, *Gila*, *Ameiurus* (Baumgartner, 1982), and a rich record of *Gasterosteus* evolution described by Bell (1994) (see number 128, below).

90. **Oncorhynchus mykiss gairdneri* Richardson (redband trout of the inland Columbia River and Oregon Lakes basins). The redband trout of the Columbia Basin between the Cascade Range and upstream barrier falls are closely related to the redband trout of the Oregon Lakes division of the Great Basin and those of Goose Lake in Oregon and California (Figure 9; Behnke, 1992, map). Unusual variation exists within and among the many populations of the redband subspecies *O. m. gairdneri*. The fish typically have 130–170 large scales in the lateral line (mean = 135–160), 63–66 vertebrae, zero to many basibranchial teeth, 18–24 (mean = 20) gill rakers, 30–50 pyloric caeca, 58 chromosomes, intermediate-sized spots and parr marks, variable cutthroat marks, and light-colored tips on the dorsal, anal, and pelvic fins (Behnke, 1992). Some of this variation (especially in basibranchial teeth and cutthroat marks) is shared with cutthroat trout, *O. clarki*. Many populations of redbands were originally regarded as *O. clarki* (Cope, 1889; Snyder, 1908; Hubbs and Miller, 1948b). In particular, the trout of the Fort Rock Basin frequently have a high basibranchial tooth count (Behnke, 1992) and are more like *O. clarki* than *O. mykiss*, as were their Pliocene and Pleistocene ancestors in the basin (see below). The general trend of redband characters is, however, less like *O. clarki* and more like *O. mykiss*. Cope (1879) and Behnke (1992) identified redband trout populations as *O. mykiss*.

All authors have agreed that the populations in question show composites of cutthroat trout and rainbow trout characters, but each has offered different ideas about whether the mixture was plesiomorphic or the product of ancient or post-introduction introgression. Gilbert and Evermann (1894) and Needham and Behnke (1962) regarded redband trout to be the product of introgression. Redband trout have been reported (Behnke, 1992) from the McCloud drainage (northern California home of hatchery rainbows), from the Goose Lake drainage of the Sacramento system, and from five desert basins of the "Oregon Lakes system" (Snyder, 1908; Allison, 1940; Hubbs and Miller, 1948:67), namely, the Harney–Malheur, Fort Rock Valley, Catlow Valley, Lake Chewaucan, and Warner Lakes. These are west and north of the basins containing *O. clarki*, namely, Alvord and Whitehorse Basins (Legendre et al., 1972; Legendre, 1976; Smith, 1978; Behnke, 1992). Hubbs and Miller (1948b) described the close relationships of trouts, minnows, and suckers to the pluvial lakes in these basins.

The Harney–Malheur and Catlow Valley basins (central Harney County, Oregon) were occupied by Malheur and Catlow Lakes, respectively, in the late Pleistocene and possibly many times earlier. The Harney–Malheur Basin fishes are derived from two different colonizations, as documented by Bisson and Bond (1971): (1) the John Day River connection with the Co-

lumbia River to the north; and (2) the Malheur River connection east to the Snake River, dated to have occurred less than 1 Ma (Luedke and Smith, 1982). The Harney–Malheur Basin possibly received drainage from Catlow Valley in pluvial times, but this neighbor to the south is now isolated (Allison, 1982) and nearly fishless. Catlow Valley lost the heads of its eastern tributaries to capture by Donner and Blitzen Creeks of the Malheur Lake basin on the west side of Steens Mountain in southeast Harney County. The trouts in these two drainage basins are similar, but those from Catlow Valley have larger scales, as expected for the more southern fish in a cline. Behnke (1992) regarded the native inhabitants of these basins to be redband trouts. This conclusion is supported by testimony from older inhabitants of Steens Mountain, indicating that native redband trout were in Home, Three-Mile, and Skull Creeks in the Catlow Basin (west of Steens Mountain) as early as 1917. By contrast, these residents noted, cutthroat trout were native on the east side of Steens Mountain (letter from Stanley Jewett to Carl Hubbs, 13 Jan 1937). The Catlow Valley redband trout in the UMMZ (collected by S. Jewett in 1936–1937) have 20–22 gill rakers, large, posteriorly concentrated spots, and no basibranchial teeth.

Holocene redband trout examined by Behnke from the Fort Rock drainage were variable, with an intermediate frequency of basibranchial teeth that is expected in products of introgression or plesiomorphic character retention. As a consequence of this mixture of characters, we conclude that the Fort Rock trout (ancient and modern) are not cladistically diagnosable as *O. clarki* or *O. mykiss*. They possess a mixture of the characters of *O. mykiss* and *O. clarki* from the various Oregon lakes. Apparently, as *O. clarki* and *O. mykiss* were diverging elsewhere in the Pliocene and Pleistocene, a mixture of ancestral characters were only partially sorted out in the Oregon Lakes system, possibly under the influence of gene flow from the north and south. The population remained mixed in the Fort Rock Basin. A relative of †*O. lacustris* also apparently inhabited the Fort Rock Basin in the Pliocene. The reports of Pacific salmon in the Fort Rock Basin (Hubbs and Miller, 1948b) are based upon bones of redband trout (Allison and Bond, 1983).

The redband trouts of the Warner Lakes (pluvial Lake Coleman; Allison, 1982) and nearby Chewaucan Basin in southern Lake County, Oregon, tend to have slightly fewer vertebrae and more gill rakers, indicating closer relationships to the Goose Lake (Sacramento drainage) redband trout (Behnke, 1992).

91. *Oncorhynchus mykiss aquilarum* Snyder (Eagle Lake trout). These fish were recognized by Snyder (1917a) and Behnke (1972, 1992) as a population of rainbow trout, *Oncorhynchus mykiss*, that possibly transferred from the Pit River drainage to Eagle Lake by a stream capture in Lassen County, California. Hubbs and Miller (1948b) identified *O. m. aquilarum* as a hybrid between native *O. clarki* and introduced *O. mykiss gairdneri*, redband trout.

Fossils resembling Pliocene *Oncorhynchus lacustris* of the Snake River Plain were collected by Taylor and Smith (1981)

and by Charles Dailey of Sierra College in deformed Pliocene sediments at "The Island" of Honey Lake, south of Eagle Lake in the northwestern part of what is now the Lahontan drainage. Although the Honey Lake fossils are not necessarily directly related to the Eagle Lake trout, both *O. m. aquilarum* and *O. lacustris* have mixtures of *O. clarki* and *O. mykiss* characters. The morphological and geographical circumstances are important because the diagnostic fossil maxillae (round in cross section) indicate the Pliocene presence of *O. lacustris* or *O. mykiss* characters in the area. The Honey Lake sediments also contain two species of *Catostomus* and one species each of *Chasmistes*, *Mylopharodon*, *Klamathella* (with two rows of pharyngeal teeth), and *Siphateles* (with a single row of teeth). The exact hydrographic relationship of the highest stages of Eagle Lake to the Lahontan Basin is hidden in several possible shorelines above and below the rim of Eagle Lake basin, which have been summarized by Hubbs and Miller (1948b:37–38). Observations on recent shorelines and connections are not necessarily relevant to the history of these fishes, however. It is possible that the rainbow trouts called *O. m. aquilarum* are relicts of the ancient redband trout of the Snake River–Sacramento River drainage of the early Pliocene and are part of the series of redband trouts of the Oregon Lakes System, described above. Two *Oncorhynchus* maxillae from Secret Valley (Madeline Plains, Modoc County, California) sediments (Wagner et al., 1997) establish the presence of a trout similar to the *O. clarki*–*O. mykiss* series north of Eagle and Honey Lakes in the Pliocene. A left dentary from Savage Canyon in the Mineral Mountains, Mineral County, Nevada (MVP 58685), most closely resembles *O. lacustris*.

92. **Oncorhynchus clarki* (Richardson) (cutthroat trout). These are inland trout of the Rocky Mountains (Figure 9). They are the only native trout of the Bonneville and Lahontan Basins, as well as of the Alvord and Whitehorse Basins located east of Steens Mountain, Oregon (Figure 9). But as noted above, redband populations west of Steens Mountain and in parts of the lower Columbia River basin possess *O. clarki* characters in varying amounts. Cutthroat trouts possess more primitive character states than other *Oncorhynchus*, and their morphological characters are predominant in the older (ancestral) fossil record. This assessment was based upon a cladistic analysis (Stearley and Smith, 1993), which included a trout specimen collected by Michael Bell from the late Miocene–Pliocene Truckee Formation (see number 89, above) and other trouts from this portion of western Nevada (LaRivers, 1964, 1966). *Oncorhynchus clarki* fossils occur in Pliocene strata in the Carson Sink, Churchill County, Nevada, portion of the Lake Lahontan area. Fossil bones of *O. clarki* were found in Pliocene sediments in the Mopung Hills, in the central part of the Lahontan Basin drainage (associated with Pliocene mollusks, Taylor and Smith, 1981); in Savage Canyon, Cedar Mountains, Mineral County, Nevada (UCMP 58685); and in pre-Lahontan sediments in Sunshine Amphitheater northwest of Walker Lake, Nevada, by Marith Reheis (USGS). A large

sample of cutthroat trout bones from the Humboldt River canyon, in sediments below the Lava Creek tephra (665 Ka), is herein diagnosed as *O. clarki* by the following characters: the anterodorsal strut of the posttemporal is tapered, not spatulate; the median shelf of the anterior portion of the dentary approaches horizontal; and the ascending wing of the premaxilla is high anteriorly. Trout scales were recovered from the Owens Lake core at levels dated at 730 and 695 Ka (Firby et al., 1997). Molecular relationships of *O. clarki* are discussed below (numbers 93–99) and are shown in Figures 10 and 14; interpopulation genetic distances are shown in Tables 2 and 3.

93. **Oncorhynchus clarki henshawi* Gill and Jordan (Lahontan cutthroat trout). The Lahontan cutthroat trout inhabits Pyramid Lake and its tributaries, except the Humboldt River (inhabited by an unnamed subspecies) and Silver King Creek of the East Fork of the Carson River (*O. c. seleniris*, Paiute trout) (Behnke, 1992:111). These several populations form a group of three subspecies that are related to the (unnamed) Alvord Basin and Whitehorse Basin subspecies (see numbers 96, 97, below), according to Behnke (1992) and our molecular data (Figure 10; Table 3).

Oncorhynchus clarki henshawi differs from its closest relatives in the Lahontan Basin in having large spots over most of the body compared with the Paiute trout, *O. c. seleniris*, which lacks spots, and it has more gill rakers and smaller scales than the Humboldt River subspecies. The other characters of this trio are similar to those of the Whitehorse Basin and Alvord Basin trouts (Figure 10; Behnke, 1992). The five forms differ among themselves by only 0.1% sequence divergence, according to our analysis of their mtDNA restriction sites (Table 3).

Originally, different spawning runs separated stocks in Pyramid Lake (Snyder, 1917a); an additional name, *O. c. tahoensis* (Jordan and Evermann (1896)), was applied to the "great trout" or "silver trout" from deep waters of Pyramid Lake, but Behnke (1981, 1992) found no morphological differences. Different size and color, if genetic and if characteristic of different spawning runs, would be evidence of significant (probably intralacustrine) differentiation.

Oncorhynchus clarki henshawi is among Holocene fossils from shore-face sediments around Pyramid and Winnemucca Lakes and from various Indian midden sites reported in the archaeological literature. These records provide documentary evidence and osteological material of the Holocene form for study; otherwise, museums lack adequate specimens from the period before the nineteenth century introductions, hybridization, and destruction.

94. *Oncorhynchus clarki seleniris* (Snyder) (Paiute cutthroat trout). This trout is limited to a few headwaters in Silver King Creek of the East Carson drainage in Alpine County, California. It differs from *O. c. henshawi* only in the absence of spots. There is no evidence pertaining to the time of its isolation, except for the 0.1% sequence divergence (Table 3) from the other Lahontan Basin trouts. We assume that cutthroat trout inhabited the stable environments of the East Carson

drainage and other mountain streams in the Lahontan Basin throughout the Miocene to Pleistocene because of the fossil record of *O. clarki* and its ancestors in the basin, extending back to the Miocene.

95. *Oncorhynchus clarki* subsp. (Humboldt cutthroat trout). Behnke (1992) pointed out the distinctiveness of cutthroat trout of the Humboldt River, relative to those of the Walker Lake, Truckee River, and Carson Valley drainages. The Humboldt cutthroat trout tends to have larger scales and fewer gill rakers, as expected for fish inhabiting warm, fluvial waters. It also has distinctive mtDNA (Williams, 1990, cited in Behnke, 1992), except in the Quinn River, where trout with Humboldt morphology have mtDNA characteristic of trout of the Lahontan Basin drainage. Behnke (1992:119) analyzed possible isolation dates in the context of the main dates of drainage separations, 13–10 Ka (Benson and Thompson, 1987), and he concluded that the divergence of the Humboldt form from *O. c. henshawi* dates from an earlier time, which is consistent with the 0.1% sequence divergence. The type specimen of the Pliocene *O. cynoclope* (LaRivers) is from the range of this subspecies, indicating an ancient local ancestry for the clade, but it lacks sufficient characters to clarify the ancestry of this subspecies.

96. *Oncorhynchus clarki* subsp. (Alvord cutthroat trout). These trout were collected by Hubbs from Virgin Creek in 1933 and Trout Creek in 1934, in southeastern Harney County, Oregon. Hubbs' field notes indicate that hatchery-raised rainbow trout were introduced into Virgin Creek as early as fall, 1933. Behnke (1992) indicated that Alvord cutthroat trout were similar to Lahontan cutthroat trout (*O. c. henshawi*) but had fewer spots, rosier sides and opercles, larger scales, fewer pyloric caecae, and fewer basibranchial teeth (Behnke, 1981, 1992). The rosy color is reminiscent of red-band trout (*O. m. gairdneri*) (Tol and French, 1988). Mitochondrial DNA restriction sites indicate that the Alvord trout is the sister subspecies to the Whitehorse trout (*O. clarki* subsp.) (Figure 10). Protein allele frequencies of Alvord trout (Tol and French, 1988) did not differ from frequencies of *O. c. henshawi* at five diagnostic loci, but all of the specimens showed introgressive influence from *Oncorhynchus mykiss*.

Tol and French (1988) suggested that Alvord trout were derived from the Lahontan (Quinn) drainage to the south, via Summit Lake, or were introduced. Behnke (1992:123) concluded that the Alvord trout was derived from Lahontan cutthroat trout in the late Pleistocene, assuming that a Wisconsinan connection was the first to provide access. This is consistent with mtDNA divergence of 0.1% (Table 3). The other fish lineage in the Alvord Basin, *Siphateles alvordensis*, may have been derived from the Lahontan *Siphateles* in the Pliocene. It is probable that both species would have used an existing connection; if one colonized earlier, it would probably have been the trout. Older Alvord "Trout Creek" sediments (now elevated) contain Miocene sunfish (Smith and Miller,

1985), but these were deposited in an earlier basin and are unrelated to the trout problem.

97. *Oncorhynchus clarki* subsp. (Whitehorse cutthroat trout). This form lives in the Coyote Lake drainage in southern Harney County, Oregon. It bears polymorphic mtDNA haplotypes, namely the Lahontan and Quinn (not Humboldt) haplotype and a unique haplotype (Williams, 1990, in Behnke, 1992). Its mtDNA is similar to that of Alvord trout. Whitehorse trout share most morphological characters (except fewer pyloric caeca) with Humboldt cutthroat trout and (except for fewer gill rakers) Lahontan trout (Behnke, 1992). Behnke (1992) contrasted the Whitehorse trout with the morphologically dissimilar Alvord trout and determined that the Whitehorse trout has fewer gill rakers, smaller scales, more pyloric caeca, more basibranchial teeth, and more spots than the Alvord trout. The two are similar in their mtDNA, however. The distribution of morphological characters, as well as the isolated position of the Whitehorse Basin, suggests that the Whitehorse trout could represent the most plesiomorphic form in the Lahontan–Humboldt–Alvord series.

The Whitehorse trout and Alvord trout characters require a connection to *O. clarki* of the Humboldt River drainage. According to sedimentary data (see Minckley et al., 1986:562; Reheis and Morrison, 1997), the lake beds of Alvord and Whitehorse Lakes (1231 m; 4040 ft) would have been inundated by one of two middle Pleistocene Eetza highstands of Lake Lahontan (with shoreline altitudes more than 1400 m (4600 ft)). The mtDNA molecules of the five subspecies of *O. clarki* from the Lahontan Basin and Whitehorse/Willow Creek drainages are similar to each other at the 0.1% level. The estimated rate of divergence (0.5% per 1 My; Figure 14) suggests that these populations were connected 200 Ka. (The most recent Eetza highstand is dated as just prior to the 150 Ka Wadsworth tephra (Reheis and Morrison, 1997).) Subsequent character sorting is responsible for the similarities and differences between Alvord trout and Whitehorse trout. Headwater capture has been important to the distribution of this form (Behnke, 1979). Lower Whitehorse Creek and its tributary, Willow Creek, flow north out of the Trout Creek Mountains to the dry lake floor 12 miles east of the Alvord desert. The drainage pattern (USGS 1:250,000 series, Adel Sheet, 1955) indicates two captures: (1) the headwaters of Whitehorse Creek were captured by McDermitt Creek (T. 40 S., R. 39. E.), a tributary to the Quinn River (Humboldt River drainage); and (2) the headwaters of Trout Creek (T. 39 E., R. 37 W.) were apparently headwaters of Willow Creek (T. 39 S., R. 37 E.) prior to their capture at Flagstaff Butte by Trout Creek, a tributary to Alvord Lake.

The Lahontan–Alvord–Whitehorse clade (Figures 9, 10) is the sister group to the Westslope cutthroat trout, *Salmo clarki lewisi*, from the Columbia Basin (e.g., Fish Lake, Wing Creek, and Cougar Creek, Idaho), from which they differ by 0.7%–0.9% sequence divergence (implying they were hydrographically connected 1.6 Ma). *Oncorhynchus c. lewisi* is

represented by relict populations throughout the Columbia River drainage, including as far south as the Boise River drainage near Atlanta, Idaho (UMMZ 234336 with cutthroat trout marks and *O. clarki* osteology). The distribution and mtDNA of Lahontan Basin and Columbia Basin trouts support an early Pleistocene connection between the Lahontan Basin and Columbia River drainages, as hypothesized by Reheis and Morrison (1997), but the other species in the two faunas are too different to support a direct spillover from Lake Lahontan to the Snake River drainage. Together, *O. c. lewisi* and *O. c. henshawi* and their relatives are the sister group to *Oncorhynchus clarki clarki*, from which they differ by 1.3%–1.8% sequence divergence, implying separation occurred about 3 Ma (Figure 10; Table 3).

98. **Oncorhynchus clarki utah* Suckley (Bonneville cutthroat trout). The Bonneville Basin contains 41 populations of cutthroat trout (Duff, 1988) differentiated into three kinds: Bonneville, Snake Valley, and Bear River (Loudenslager and Gall, 1980; Martin et al., 1985; Behnke, 1992). They were characterized by Behnke (1992) as subdued in coloration, 133–183 (160) lateral scale rows, 33–46 (38) scales above the lateral line, 16–24 (19) gill rakers, 25–54 (35) pyloric caeca, and 1–50 basibranchial teeth in at least half the population (Hickman, 1978; Duff, 1988). The counts are basically those of the Yellowstone cutthroat trout, *O. c. bouvieri*. Mitochondrial DNA restriction-site analysis indicates that the Bonneville trouts, exclusive of the Bear River forms, are the plesiomorphic sister group to all other *O. clarki* (Figure 10), differing from them by 1%–4% sequence divergence (Table 3). The Deaf Smith Creek (Salt Lake County, Utah) population differs from other Bonneville cutthroat trouts in its mtDNA (sequence divergence >2% from other Bonneville cutthroat trouts and 3%–4% from all other cutthroat trouts; Table 3). The Bonneville cutthroat form shares a protein allele with the Colorado River subspecies (Martin et al., 1985; Shiozawa and Evans, unpublished data) and has representatives in Santa Clara River headwaters in Pine Valley in southwestern Utah (see “Discussion”). Fossil cutthroat trout are known from the late Pleistocene Black Rock Canyon locality (shoreline dated at 11,000–13,000 years B.P.) in northeastern Bonneville Basin (Smith et al., 1968); from Homestead Cave, 10,160–11,170 years B.P. (Broughton, 2000a, 2000b); and from the late Pleistocene Old River Bed between the northern Bonneville and Sevier Basins (Oviatt, 1984).

99. **Oncorhynchus clarki* subsp. (Snake Valley cutthroat trout). The Snake Valley cutthroat trout forms tend to have more spots than other Bonneville cutthroat trouts. Behnke (1992) suggested that trouts were possibly absent from the Bonneville Basin until the late Pleistocene, and Duff (1988) postulated they had an insufficient time of isolation to become a distinct species. We interpret the cladistic primitiveness of the diversity in the Bonneville Basin and the level of divergence of the Bonneville cutthroat trout forms to indicate an ancient, possibly Miocene, presence of cutthroat trout in what

became the Bonneville Basin. Fossils from 12 Ka or older have been reported from Smith Creek Canyon in Snake Valley (Mead et al., 1982).

100. *Oncorhynchus clarki* subsp. (Bear River cutthroat trout). The Bear River form shares proteins and mtDNA with the Yellowstone cutthroat trout, which is consistent with its former connections to the Snake River, between 140 Ka and 80 Ka (Bouchard et al., 1998). The Bear River and Thatcher Basin were most recently diverted to the Bonneville Basin system about 20 Ka (Bright, 1966, 1967; Bouchard et al., 1998). The Bear Lake relative of the Bear River form has more pyloric caecae, an azure blue color that is dense on the snout but diminishes posteriorly, and yellowish fins (Nielson and Lentsch, 1988). The Bear Lake form is distinct in its life history, reproductive separation, and coloration (Nielson and Lentsch, 1988; Behnke, 1992). The Bear River form is the sister group to the Yellowstone River and Snake River populations (Figure 10), differing from them at the 0.3%–0.4% level in its mtDNA restriction sites (Table 3). These populations differ from *O. clarki utah* of the main Bonneville Basin system at the 1.4%–3.5% level, indicating their separate evolution through most of the Pleistocene.

CYPRINODONTIDAE

101. *Cyprinodon radiosus* Miller (Owens pupfish). This species inhabits the Owens River valley, which is a tributary to Owens Lake, Mono County, California. It is the sister species to *C. macularius* of the lower Colorado River drainage (Echelle and Dowling, 1992; Echelle and Echelle, 1993; Figure 11); it differs from that species by 2.8% sequence divergence of mtDNA (Table 4). *Cyprinodon macularius* and *C. radiosus* are related to various species of pupfishes from the Death Valley system (Miller, 1946a, 1948) and northern Mexico (Figure 11). *Cyprinodon radiosus* is similar to *C. macularius* in having seven pelvic-fin rays, dorsal origin at the midbody, and disrupted vertical bars in females, but it shares an apomorphic scale structure with the Death Valley species (Miller, 1943b, 1948). It is additionally characterized by having large scales and a large, deep body, like *C. nevadensis*; its long dorsal and anal fins and long prehumeral length resemble those of *C. diabolis*. Male coloration is unique, with amber-colored margins on the dorsal and anal fins and a pale or amber-colored (not black) terminal band on the caudal fin.

Cyprinodon nevadensis Eigenmann and Eigenmann (Amargosa pupfish). This is a geographically variable and widespread pupfish in the Death Valley system. It is found in numerous springs from Ash Meadows in Nye County, Nevada, to Shoshone, Tecopa, and Saratoga Springs and other localities along the Amargosa River near the boundary of Inyo and San Bernardino Counties, California (Miller, 1948). The species is large and deep, with large scales, preorbital scales; broad, rounded, incised outer tooth-cusps; six pelvic-fin rays; and the dorsal-fin origin usually behind the midbody. Males are deep

blue with a dark terminal border on the pale caudal fin; females have continuous vertical bars. Protein and mtDNA evidence shows the *C. nevadensis* group (Figure 11) to be related to *C. salinus*, *C. diabolis*, and *C. milleri*, with evidence of possible introgressive homoplasy (Echelle and Dowling, 1992; Echelle and Echelle, 1993).

102. *Cyprinodon nevadensis nevadensis* Eigenmann and Eigenmann (pupfish). This subspecies, from Saratoga Springs in southern Death Valley, California, is characterized by its robust body shape; high, narrow scales; numerous radii; and dense reticulations (Miller, 1948).

103. *Cyprinodon nevadensis amargosae* Miller (pupfish). This subspecies is from the Amargosa River in San Bernardino County, California, including Death Valley. Small scales with few radii characterize it. Miller (1948) recognized several isolated populations as different races.

104. *Cyprinodon nevadensis callidae* Miller (pupfish). This subspecies, from Tecopa Hot Springs along the Amargosa River in Inyo County, California, is diagnosed by large scales, narrow interorbital distance, and a short caudal peduncle (Miller, 1948).

105. *Cyprinodon nevadensis shoshone* Miller (pupfish). This subspecies is from Shoshone Springs, Inyo County, California. It is characterized by a narrow, slender body and relatively straight ventral profile (Miller, 1948).

106. *Cyprinodon nevadensis mionectes* Miller (pupfish). This subspecies is from Big Spring, Ash Meadows, Nye County, Nevada. Miller (1948) diagnosed it by its small size, few scales and fin rays, narrow body, posterior dorsal fin, long head, and arched predorsal profile. There are several distinct races.

107. *Cyprinodon nevadensis pectoralis* Miller (pupfish). This subspecies is from near Lovell's Spring, Ash Meadows, Nye County, Nevada. Small scales, large number of pectoral-fin rays, and robust body shape characterize it (Miller, 1948).

108. *Cyprinodon salinus* Miller (Salt Creek pupfish). This isolated species inhabits Salt Creek canyon, northern Death Valley, Inyo County, California (Miller, 1943a). A median ridge on the teeth, slender body, small scales, and scaleless preorbital region characterize it. It is similar to *C. nevadensis* and *C. milleri*, with which it shares small fins, especially the pelvics, posterior position of the dorsal fin, small head and eyes, and dark blue color. Miller (1946a) outlined geological evidence that the divergence of *C. salinus* and *C. nevadensis* occurred in the interval since isolation of the Salt River by the desiccation of Lake Manly, which was estimated at that time to be about 20 Ky (but see *C. milleri*, below). It is related to *C. nevadensis* and is the sister group to *C. milleri*, according to protein evidence (Echelle and Echelle, 1993). Molecular data indicate that *C. salinus* is the sister group to the other Death Valley and Ash Meadows species (Echelle and Dowling, 1992; Figure 11). *Cyprinodon salinus* does not differ from *C. milleri* in its mtDNA, but these two differ from *diabolis* + *nevadensis*

by 0.13% sequence divergence, indicating more than 10 Ky of divergence.

109. *Cyprinodon milleri* LaBounty and Deacon (Cottonball Marsh pupfish). This distinctive species was discovered living under most severe conditions in a marsh near Salt Creek, several miles southeast of the type locality of *C. salinus* in Death Valley, Inyo County, California (LaBounty and Deacon, 1972). The population lives below sea level in waters that experience a temperature range of 0°–40° C. The fish can survive a salinity range of 0–78 g/L. Large teeth, reduced or absent pelvic fins, reduced lacrimal pores, short, slender caudal peduncle, small fins, and small scales diagnose the species. The large, tricuspid teeth have a broad, spatulate central cusp with no ridge on the outer face and a slim central shaft, like that of *C. macularius* Baird and Girard but with deeper incisions separating the outer cusps. It shares the absence of preorbital scales with *C. salinus* and *C. diabolis*; it shares small scales and a slender body with *C. salinus*. *Cyprinodon milleri* and *C. salinus* differ at 4 of 31 protein loci (Rogers genetic distance <0.06) according to Echelle and Echelle (1993), but the mtDNA of *C. salinus* and *C. milleri* do not differ. The documentation of morphological differences by LaBounty and Deacon (1972) showed *C. milleri* to be the most phylogenetically derived species in Death Valley. LaBounty and Deacon (1972) and Minckley et al. (1986) hypothesized an isolation interval of only a few hundred years, assuming no heterogeneity at the time of the most recent hydrological connections documented by the geological studies of Hunt and Mabey (1966) and Hunt et al. (1966). This is consistent with the 0% sequence divergence and with geography, but it is in conflict with protein and morphological differences. Introgressive homoplasy of mtDNA is possible, in light of this inconsistency. The time of divergence is therefore ambiguous, but this is a possible example of rapid evolution.

110. *Cyprinodon diabolis* Wales (Devils Hole pupfish). Devils Hole is a small cave fault that opens at an elevation of 2488 ft, in Ash Meadows, Nye County, Nevada. Its pool is the sole range of the 200–400 individuals of *Cyprinodon diabolis*. This small species has no pelvic fins, long dorsal and anal fins, a posterior dorsal fin, a convex caudal fin, and no preorbital scales. Mature males have a black terminal band on the caudal fin; mature females lack vertical cross bars and show reversal of some sexually dimorphic characters (Miller, 1948). The population has lost individual territorial behavior (Liu in Turner, 1974). Mitochondrial DNA data (Figure 11) indicate that *Cyprinodon diabolis* is related to the *C. nevadensis* clade, and it shares most of its characters (e.g., large scales) with *C. nevadensis*; however, it shares two strikingly nonreductive characters, increased dorsal- and anal-fin rays, with *C. radiosus*. Turner (1974) electrophoretically analyzed 31 presumptive loci and found *C. diabolis* to be similar to *C. nevadensis* and *C. radiosus* at the 0.968 and 0.936 levels of similarity, respectively. Morphological and mtDNA

homoplasies in combination suggest reticulate evolution in the history of *C. diabolis* (Echelle and Dowling, 1992).

111. †*Cyprinodon breviradius* Miller (pupfish). This fossil form was found with *Fundulus curryi* in Titus Canyon on the east side of Death Valley, Inyo County, California (Miller, 1945b). The age was estimated by McAllister to be Miocene (Miller, 1981), but it could be Pliocene (see number 117, below). It is similar to *C. macularius*, but it has a slender body, like *C. salinus*, and 20 caudal vertebrae, which is several more than normal for the Death Valley group. On the basis of these apomorphies, the fossil is assumed to be ancestral to the ancestor of the *C. fontinalis*–*salinus*–*diabolis*–*nevadensis* clade in Figure 11. This clade differs from its sister species by an average of 2.9% sequence divergence.

GOODEIDAE

112. **Empetrichthys merriami* Gilbert (Ash Meadows poolfish). This species, now extinct, was taken in five separated springs in Ash Meadows, Nevada. It was a small, robust fish with a deep body, large head, narrow mouth, and molariform pharyngeal teeth (Miller, 1948; Uyeno and Miller, 1962). Apparently always rare, it was possibly eliminated by scientific collecting (Miller, 1948:101).

113. **Empetrichthys latos* Miller (Pahrump poolfish). This species lived in three springs in Pahrump Valley, Nye County, Nevada. Each spring had a distinct subspecies. Miller (1948) and Uyeno and Miller (1962) distinguished it from *C. merriami* by its slender body, broad and weak mouth, pointed teeth, and smaller scales. Springs that were inhabited by the three subspecies are geographically close to each other, and the taxa are morphologically similar. They differ from each other in body and fin shapes. A fossil relative, †*Empetrichthys erdisi* (Jordan), from Pliocene sediments in the Ridge Basin, Los Angeles County, California, had conical teeth, smaller scales, and more vertebrae (Uyeno and Miller, 1962). *Empetrichthys* pharyngeals were identified by W.L. Minckley from the Glendale Formation (locality in Van Devender and Tessman, 1975) in southern Nevada (Minckley et al., 1986:582).

114. *Crenichthys baileyi* (Gilbert) (White River springfish). This species inhabits springs in the Pahrnagat Valley and tributaries to the White River, in Clark, White Pine, Nye, and Lincoln Counties, Nevada. Geographic variation was recognized, and four subspecies were named by Williams and Wilde (1981).

115. *Crenichthys nevadae* Hubbs (Railroad Valley springfish). This species differs from *C. baileyi* primarily in coloration. It lives in Hot Springs in Railroad Valley and tributary Duckwater Valley, Nye County, Nevada. This drainage was probably connected to the Pahrnagat Valley and the White River system through the Penoyer and Desert Valleys (Hubbs and Miller, 1948b).

FUNDULIDAE

116. †*Fundulus nevadensis* (Eastman) (killifish). This is a late Miocene species (from at least 6 Ma) from the Truckee Formation in the Lahontan Basin near Hazen, Nevada. It is a long, slender fish with 11 or 12 dorsal-fin rays, the dorsal fin well in advance of the anal fin, 10–13 anal-fin rays, and small, circular scales in more than 65 lateral rows (Eastman, 1917; Miller, 1945b). LaRivers (1964) reported it in correlated beds in the Sahwave Mountains, Pershing County, Nevada.

117. †*Fundulus curryi* Miller (killifish). This species, from the east side of Death Valley, was similar in some ways to *Empetrichthys* (Miller, 1948:100). It is a short (44–66 mm SL), deep fish with 14 or 15 dorsal-fin rays, the dorsal fin much closer to the anal fin than to the pelvic fins, 15 or 16 anal-fin rays, a broadly rounded anal fin, and scales like those of *F. eulepis* (Miller, 1945b). Numerous specimens of *Fundulus* have been collected from Titus Canyon, Death Valley, California. Their ages are uncertain. The lower part of the Titus Canyon Formation has been dated as early Oligocene; the date was based upon the presence of *Mesohippus*, titanotheres, hydracodont rhinoceros, artiodactyls, and rodents, as well as on radiogenic dates (Saylor, 1994). But if *F. curryi* was collected near *Cyprinodon breviradius* Miller, it could be Miocene or Pliocene (Miller, 1945b). An old specimen of *Fundulus* was recently collected at the Bullfrog Mine, southeast of Beatty, Nevada. It was found in a dark gray to black shale beneath a late Oligocene to early Miocene volcanic unit dated at 23 Ma.

118. †*Fundulus eulepis* Miller (killifish). This species is from beds of Pliocene age in Death Valley near Furnace Creek. The specimens are relatively long (~9 cm SL), with 13 or 14 dorsal- and anal-fin rays, the dorsal fin in advance of the anal fin by about one-third of the distance from the anal fin to the pelvic-fin origins, and about 45–50 lateral scale rows (Miller, 1945b).

119. †*Fundulus* spp. (killifishes). Undescribed samples of *Fundulus* have been collected from three localities on the Nevada Test Site by Richard V. Wyman (of the University of Nevada, Las Vegas) and others. Specimens studied so far are large (up to 9 cm SL), with conical teeth, 13 rays in the dorsal and anal fins, the dorsal fin slightly in advance of the anal fin, 6 pelvic-fin rays, moderately small scales on the body, scaled cheeks, and 20 caudal vertebrae. The caudal peduncle is moderately long, like that of *F. eulepis*. They lack evidence for modification of the anal fin, as seen in Goodeidae. *Cyprinodon* and *Fundulus* in the Miocene and Pliocene of the Great Basin are similar in morphology and diversity to modern cyprinodontoids (*Empetrichthyines*, *Cyprinodon*, *Fundulus*) in the southwestern United States. The fossil *Fundulus* add to the evidence of widespread, warm, low-gradient habitats during the Miocene.

120. †*Fundulus* spp. (killifishes). *Fundulus* have been collected from two localities in the Esmeralda Formation, or beds reported to be Esmeralda Formation northwest of Death Val-

ley. These locations are in different and younger rocks than the Siebert tuff in which *Fundulus lariversi* was found.

121. †*Fundulus davidae* Miller (killifish). A single specimen (Cal. Tech. 10276) of this species was obtained through Lore David from an oil driller. The specimen is from the Mohave Desert in northwestern San Bernardino County, California, but the formation of origin was not known. Miller (1945b) judged that the fossil was of Pliocene or early Pleistocene age. The specimen is short and moderately deep, with 11 or 12 dorsal and anal-fin rays, 6 pelvic-fin rays, a large head, 40–45 lateral scale rows, and scale features like those of *F. eulepis*. Some of the characters are similar to those of *Empetrichthys erdisi* (Miller, 1945a). Specimens figured by Pierce (1959) from the Miocene Barstow Formation near Yermo in the Mohave Desert, might be *Fundulus* (Uyeno and Miller, 1962); the supposed fossil fish eggs reported from this locality were shown to be ostracods (Hubbs and Miller, 1962).

122. †*Fundulus lariversi* Lugaski (killifish). This species was described from the Siebert tuff (which formed 17 Ma), from Tonopah, Nye County, Nevada. It is characterized by a slender body, conical teeth, dorsal fin over anal fin and half way between snout and caudal tip, 11 dorsal-fin rays, 13 anal-fin rays, 12 pectoral-fin rays, pelvic fin reduced to seven rays, 17 caudal-fin rays, and 31 vertebrae. This species is similar to *Empetrichthys* (Lugaski, 1978), but it possesses a pelvic fin.

123. †*Fundulus* sp. (killifish). *Fundulus* was collected from the middle Miocene Humboldt Formation north of Wells, Nevada. The specimen is deposited at the Mackay School of Mines, University of Nevada, Reno.

COTTIDAE

124. **Cottus beldingi* Eigenmann and Eigenmann (Paiute sculpin). This sculpin occupies the Lahontan, northern Bonneville, and Columbia–Snake drainages. Jordan (1924) reported fossils from Pleistocene cave deposits in the Lahontan Basin. Taylor and Smith (1981) reported the species from Pliocene rocks at Mopung Hills. A basioccipital diagnosed only as *Cottus* has been identified (by K.W.G.) from Pliocene sediments in Secret Valley, California, and a cottid parasphenoid was collected by Julian Humphries from Virgin Valley, Nevada. An angular–articular from middle Pleistocene sediments of the Humboldt River gorge unquestionably represents *Cottus beldingi*. R.R. Miller collected specimens from Pliocene diatomites at Fish Cave, Churchill County, Nevada. This has apparently been a Lahontan Basin cool-water species since a time when the Snake River Plain had a strikingly different sculpin fauna (Smith, 1987) and the central Columbia Basin had a warm, lowland fauna lacking sculpins (G.R. Smith et al., 2000).

125. **Cottus bairdi* Girard (mottled sculpin). This is the abundant, widespread sculpin of the Snake–Columbia and Bonneville drainages (as well as of eastern North America). Two different forms are found in the Harney–Malheur drainage (Bisson and Bond, 1971). The two morphs possibly colonized

from the Columbia River drainage (by stream capture from the John Day River) and from the upper Snake River drainage (prior to separation of the Harney–Malheur drainage from the Snake River drainage). Pleistocene fossils were reported from the Black Rock and Hot Springs localities of Lake Bonneville (Smith et al., 1968). A Pliocene or Pleistocene *Cottus* was collected from Park Valley, Box Elder County, Utah (Felix, 1956), by Ted Cavender.

126. **Cottus extensus* Bailey and Bond (Bear Lake sculpin). The Bear Lake sculpin is now endemic to that lake, which is on the Utah–Idaho border, but it was common in Lake Bonneville in the late Pleistocene (Smith et al., 1968; Broughton, 2000a, 2000b).

127. *Cottus echinatus* Bailey and Bond (Utah Lake sculpin). This extinct species is known only from Utah Lake, Utah. It has not been found among Lake Bonneville fossils, but it probably shared a common ancestor with *Cottus extensus* (Bailey and Bond, 1963).

GASTEROSTEIDAE

128. †*Gasterosteus doryssus* (Jordan) (Truckee stickleback). The fossil three-spined stickleback (*Gasterosteus doryssus*) occurs in the Great Basin in the Miocene Truckee Formation in west-central Nevada from Hazen (Bell, 1974) to the Sahwave Mountains (LaRivers, 1964). It represents a lowland fauna from the late Miocene (Bell et al., 1985) of Nevada when the drainage was west to the Pacific Ocean. Thousands of specimens have been collected and analyzed as a premier example of rates of evolution; this data has been summarized by Bell (1994, and references therein; Figure 12).

129. **Gasterosteus aculeatus* Linnaeus (threespine stickleback). Threespine sticklebacks are recorded from late Pleistocene sediments in the Mohave Basin in association with ancient Lakes Manix and Thomson and Mohave River sediments (Roeder, 1985; Jefferson, 1991; Reynolds and Reynolds, 1991; Bell, 1994). Recently collected, living specimens of *Gasterosteus aculeatus williamsoni* from high elevation in the Mohave Basin have some males with a unique melanistic nuptial pattern, suggesting that they are native (Bell, 1982). But trout (with stray sticklebacks) were transplanted by fisheries biologists in that region in the 1930s or earlier, raising the possibility that the modern population is introduced (Leo Shapovilov, California Department of Fish and Game, in litt. to R.R. Miller, University of Michigan, Museum of Zoology; Miller and Hubbs, 1969).

CENTRARCHIDAE

130. †*Archoplites* sp. (perch). Late Miocene sunfish occur in or near the Great Basin at several localities. These include Park Valley, Box Elder County, Utah (Felix, 1956); the Salt Lake group, (MVP 117073, collected by Patrick McClellan); Windermere Hills near Elko, Nevada; the Snake River Plain in Idaho

and Oregon; and Trout Creek, Harney County, Oregon (Smith and Miller, 1985). Trout Creek specimens have been referred to the genus *Plioplarchus* Cope. Two partial dentaries of large sunfish were collected by J.A. Shotwell from the Juntura For-

mation, outside the edge of the Great Basin in Malheur County, Oregon. Other specimens are from Miocene sediments in Klamath Lake, Harney and Malheur Counties. These centrarchids are diverse and under study.

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